CHARACTERIZATION OF ROTATIONALLY GRAZED LIMPOGRASS PASTURE AND ANIMAL RESPONSE TO SUPPLEMENTATION

BY

JAMES FRANK HOLDERBAUM

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1989

To my wife, Sandra

ACKNOWLEDGMENTS

The author is grateful for the guidance, patience, and encouragement of his cochair, Dr. L. E. Sallenberger, throughout the doctoral program, and during times when the author's family was expanding. Thanks are extended to Dr. K. H. Quesenberry for his professional guidance and for helping the author through the storms. Special thanks are extended to Dr. W. E. Kunkle and Dr. B. Bates for their contributions to the design and finer points of the dissertation research. The author is especially grateful to Dr. J. E. Moore for his guidance, but mostly for encouraging the author to think. Thanks are also due to members of the staff at the University of Florida who have made the author's life easier along the way. They include Sid Jones, Dane Hernia, Nancy Wilkinson, John Funk, Debbie Schuitz, Patty Connolly, and Pete Brown. The author also recognizes Dr. R. M. Shireman for her assistance in the protein assay procedure used in the research and Steve Linda for assistance in statistical analysis. The author is grateful to C. M. Payne and Sun Seed Company for providing the saccharomyces seed used in the research and for the financial support from USDA Special Grant 86-CRSR-2-2846.

The author wishes to extend special thanks to Dr. O. C. Ruelke for his friendship, support, and interest. The author aspires to someday bring as much enthusiasm to the classroom as Dr. Ruelke has for the past thirty years.

To the numerous students who helped sort through the substance of this dissertation and contributed to the daily grind, the author is most appreciative.

To the many graduate students that the author has come to know, much appreciation is expressed for their friendship and support. Special thanks are due to Glen Aiken, Bob Allahouse, Alfonso Ortega-Santos, Jorge Morales, Antonio Flores, Sue Ellen Johnson, Cesar Chaparro, and John Russell.

To the author's parents, Paul and Janet Holderbaum, and his wife's parents, David and Shirley Pilkerton, whose encouragement, patience, love, and support are greatly appreciated. To the author's children, James Brandon, Callen David, and Grace Ann, whose presence has been the author's greatest inspiration. And finally, to his wife Sandra, whose love, support, and encouragement have made this possible and will bring even greater joy in the future.

TABLE OF CONTENTS

LIST OF TABLES

Abstract of Dissertation Presented to the Graduate
School of the University of Florida in Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

CHARACTERIZATION OF ROTATIONALLY GRAZED LIMPOGRASS
PASTURE AND ANIMAL RESPONSE TO SUPPLEMENTATION

By

James Frank Holderbaum

December 1989

Chairman: Kenneth H. Quesenberry
Major Department: Agronomy

In Florida, a slump in animal performance is usually observed sometime between late July through mid-September with cattle grazing 'Floralta' limpograss [Hemarthria altissima (Poir.) Stapf et C.E. Hubb.] (LG) pasture. Reports of low crude protein (CP) concentration in LG have led to speculation that a limitation of dietary CP contributes to low average daily gain (ADG) of cattle.

In 1987 and 1988, 84-d grazing studies were conducted to determine the effect of protein supplementation (as cornures) on ADG of steers rotationally grazing LG pasture during the summer slump period. Concurrently, LG pastures were characterized to describe changes in canopy structure and forage nutritive value and to make inferences about pasture attributes that may be contributing to the summer slump.

Nonsupplemented steers grazing LG pasture (NP) averaged 0.29 kg d^{-1} gain over the two years. Supplementing steers on LG pasture with rations containing 0.587 kg corn and 0.029 kg urea (123 g CP kg^{-1}; LO) or 0.587 kg corn and 0.116 kg urea (500 g CP kg^{-1}; HI) daily resulted in approximately a 100% increase in seasonal daily gain over that on NP. During the specific times in each grazing season when animal performance on NP was lowest, however, supplementation with corn-urea did not eliminate the summer slump. Animal daily gains were 79% higher for an LG-aeschynomene (*Aeschynomene americana* L.) association (LA) than for NP.

Whole canopy CP concentration of green herbage tended to be lowest during the period when ADG was lowest. Mean LG leaf blade CP concentration (99 g kg^{-1}) was more than twice as great as LO stem plus sheath (40 g kg^{-1}), but stem plus sheath constituted 82% of total LG herbage mass and 63% of LG total N content. Limpograss leaf blade/stem plus sheath ratio (LSR) was 3 to 5 times greater in the upper (0.4 to 0.6) than lower (0.1 to 0.2) half of the sward canopy. Neutral detergent fiber (cell wall) N represented 60 to 70% of limpograss total N and a significant amount of this N (22 to 34%) was associated with the indigestible acid detergent fiber fraction. Low steer gains on unsupplemented LG in summer appear to be related to low CP concentration, low LSR in the grazed part of the canopy, and a high proportion of plant N associated with the cell wall fraction.

CHAPTER I
INTRODUCTION

Improving animal production under grazing conditions has been the impetus behind much of the research relating to forage-livestock production systems, particularly in tropical and subtropical environments. From the forage perspective, this challenge is often met with the introduction of new and/or improved forage species that are judged to be superior to current species. 'Floralta' limpograss [Hemarthria altissima (Poir.) Stapf et C.E. Hubb.] is a tropical grass that has proved effective in improving animal production per hectare on the flatwood soils in Florida. However, as with other improved tropical grasses that have contributed to the overall improvement in cattle production systems, seasonal depressions in animal performance are often observed. From a practical standpoint, the summer slump phenomenon is often dismissed as an enemy of cattle production in the south. From a research standpoint, however, ascertaining the causal factors of the summer slump provides a unique challenge. Identifying these forage and pasture attributes that contribute to the summer slump in animal performance may provide greater insight into how we can further improve the forage aspect of livestock production systems and improve on

the selection criteria used for identifying superior cultivars.

Presented here are the results of a series of experiments that were conducted in 1987 and 1988. The primary objective was to determine if plant N (protein) plays a role in the summer slump phenomenon that is observed on limpograss pasture. The review of the literature in the following section (Chapter II) provides a description of the summer slump followed by a discussion of the properties of plant N that may affect its availability to, and utilization by the grazing ruminant. Chapter II ends with a brief discussion of increasing dietary CP intake of grazing animals with particular reference to using urea as a dietary supplement. Results from a protein supplementation study are presented in Chapter III. Chapters IV and V relate to the characterization of limpograss pasture canopy structure and nutritive value in reference to the summer slump phenomenon, and the distribution and fate of plant N in limpograss, respectively. A general discussion is presented in Chapter VI relating to the overall research, and some observations are offered.

CHAPTER II
LITERATURE REVIEW

The Summer Slump in Animal Performance

The term "summer slump" has been used to describe a period of time when a decline is observed in average daily gain (ADG) of cattle (Bos spp.) grazing summer pasture. In Florida, a summer slump in ADG is usually observed sometime between late July through mid-September on tropical grass pastures of relatively low overall quality such as limpograss [Hemarthria altissima (Poir.) Stapf et C.E. Hubb.] and bahiagrass (Paspalum notatum Flugge; Rusland et al., 1988; Sollenberger et al., 1988a).

A distinction needs to be made between the summer slump phenomenon and the general seasonal depression in animal performance observed on unimproved tropical and subtropical grass pastures during the dry or cool season (Milford, 1960; Cohen and O'Brian, 1974; Stephenson et al., 1983; Van Niekirk and Jacobs, 1985; Lee et al., 1987). In these cases, poor animal performance has been attributed to low crude protein (CP) concentration and/or dry matter (DM) digestibility and slow growth rates of grasses during this time of year (Milford, 1960; Wilson and Minson, 1980). During the summer slump in Florida, active plant growth is occurring and there

may not be a correlation between these forage quality attributes and ADG (Rusland et al., 1988).

There is much speculation as to the cause of this depression in animal performance under summer grazing conditions. Attention was initially given to environmental conditions during the summer slump period in relation to the grazing animal's well being. In the southeastern United States, and Florida in particular, the summer slump period occurs during the time of year when temperatures and relative humidity are highest and may have an adverse effect on animal grazing behavior resulting in depressed intake of forage. In a recent study, Saliahargar et al (1988b) reported that ADG of steers grazing 'Mott' dwarf elephantgrass (Pennisetum purpureum Schum.) pastures at the same location as animals grazing limpograss showed no decline in gain during the summer. Based on contrasting results between grasses, it was suggested that the summer slump on limpograss pasture was related primarily to environmental effects on limpograss herbage rather than direct effects on the animal itself (Rusland et al., 1988).

As mentioned above, low gains are characteristic responses during the summer slump period. Numerous pasture and confined feeding studies with both sheep (Ovis aries) and cattle have demonstrated that animal gain can be depressed due to a decrease in DM intake. Low energy concentration (Raymond, 1969) as well as low organic matter digestibility

(OMD· Bianter et al., 1961) in feeds have been shown to adversely affect DM intake in ruminants. Mineral imbalances or deficiencies (Rees et al., 1974; Mayland et al., 1967) can lead to a depression in feed intake. The literature has also shown that anti-quality factors (i.e., secondary metabolites, such as phenolics; Hammond, 1987) can inhibit protein digestibility (Hornman et al., 1986; Akin et al., 1987), and may (Robbins et al., 1967), or may not (Lowry and Sumpter, 1987), depress DM intake. Hence, many forage factors that affect DM intake (Moore and Mott, 1973) have been implicated in contributing to the summer slump phenomenon.

Research has shown that limiting dietary CP concentration can adversely affect DM intake (Egan, 1965; Milford and Haydock, 1965, Milford and Minson, 1966a; Weston, 1971, Ventura et al., 1975). Dietary CP concentrations below 70 g kg^{-1} (DM basis) are believed to limit animal performance (Minson and Milford, 1967), and approximately 70 g kg^{-1} CP in the diet is the minimum level required for a positive N balance in the ruminant animal (Milford and Haydock, 1965). Because of the well-established relationship between CP concentration and DM intake (Moore and Mott, 1973), much attention has been given to the limitation of dietary CP as a contributing factor to the summer slump condition. However, difficulties are encountered in assessing plant N in relation to ruminant protein requirements and its availability to, and prehension by, grazing animals. The remainder of this

section will be devoted to a discussion of assessing why and how plant N may be a factor in the summer slump in animal performance that is observed with cattle grazing limpograss pastura.

The overall working hypothesis for this dissertation research is that animals grazing limpograss are not acquiring adequate amounts of N (protein) during the summer slump period. Limited prehension of plant N by the grazing animal (Arnold, 1960) and the unavailability of plant N once ingested (Goering et al., 1972; National Research Council, 1985) can singly or jointly be associated with protein deficiencies of ruminant animals. These aspects will be discussed in relation to ruminant protein requirements under grazing conditions. Reference to plant N in lieu of plant protein is intentional on the part of the author. It is an attempt to draw attention to the fact that the preponderance of agronomic and forage research relating to total or "crude" protein concentration and content in forage is based on the quantitative analysis of plant N--not true protein. Reference to plant N will also help to introduce and elucidate the concepts of the functionality of plant N in the sward canopy and its prehension by the grazing animal, and the functionality of plant N upon ingestion by the animal.

Properties of Nitrogen in the Sward Canopy

A dominant feature of plant-animal interactions is diet selection when cattle consume pasture herbage (Raymond, 1968). The potential for selectivity is initially dependant on the canopy structure of the sward that is presented to the animal (Hannetje and Ebersohn, 1980). Canopy height (Tayler and Rudman, 1966; Stobbs, 1973a) and the proportions of leaf and stem material (Stobbs, 1973b; Wilson and Minson, 1980) within the canopy, and their bulk density (Stobbs, 1973a) all contribute to the degree of selectivity, the intrinsic availability of herbage to the animal (Alldan and Whittaker, 1970), and the ultimate prehension of plant material.

Variation in N concentration of plant material by plant part and maturity has been well documented in the literature. Nitrogen concentration (hence, CP concentration) of leaf material is generally higher than that of stems and petioles, and younger plant material often has higher N concentration than more mature herbage (Minson, 1971). Due to the relatively high percentage of stem in many tropical grasses (Wilson and Minson, 1980, Sollenberger et al., 1988a), greater anatomical and compositional variability can occur vertically through the sward canopy of tropical grasses (Hannetje and Ebersohn, 1980; Stobbs, 1973b) than with temperate species. There is potential for variability in N content vertically through the grass canopy depending on the

relative proportions of leaf and stem material and their respective N concentrations at different levels within the canopy. It is believed that animals do not selectively graze on the basis of CP concentration (Marten, 1969 and 1978). Thus, the prehension of plant N by the grazing ruminant is a function of diet selection within the sward canopy but mostly a function of the distribution of N within the sward

The term functionality or functional property has been defined as any property of a substance, besides the nutritional ones, that affects utilization (Cherry, 1981). Ironically, the term functionality has been adopted by researchers studying plant protein as a human food source. Sward canopy structure and N distribution within the canopy can be considered functional properties of prehension of plant N in the pasture. Recognition of plant N functionality in the pasture sward is a prerequisite to properly and accurately assessing the relationship between plant N and the grazing animal and for assessing the true prehension of plant N under grazing conditions

Reference to whole canopy CP concentration and/or content of both tropical (Barth et al., 1982; Ruelke and Quesenberry, 1983, Adjel et al., 1988; Christiansen et al., 1988) and temperate (Colburn and Evans, 1967; Abdalla et al., 1988a) grasses abounds in the literature. The inference that there is a direct relationship between whole canopy CP (i.e., total plant N times 6.25) and the actual utilization

(prehension and availability) of plant N by the ruminant is inherent to the reporting of whole canopy CP values. As was mentioned earlier, the relationship between CP concentration and intake has been well established and it is this relationship that has governed the appropriateness of using CP values as a determinant of forage quality.

Under grazing conditions, however, the CP concentration of a whole canopy sample does not necessarily reflect the CP concentration of herbage consumed by the grazing animal at any given point in time. With forage species that have a nonuniform distribution of N within the canopy, CP concentration of herbage consumed at any point in time rarely reflects the CP value for the whole canopy. In a rotationally-grazed alfalfa (Medicago sativa L.) pasture, N concentration of available herbage decreased each successive day during a grazing period (Arnold, 1960). Depending on the uniformity of N distribution in a sward canopy and the time frame in which the sward is grazed (stocking rate), the N concentration of herbage consumed can drastically change over time relative to whole canopy N concentration.

Due to the erect growth habit of limpograss and the high percentage of stem material, particularly in the lower canopy (Sollenberger et al., 1988a), it is likely that CP concentration of herbage consumed decreases over time within a grazing cycle in a rotational grazing system. If assessed in the context of plant N functionality in the sward canopy,

limpograss sward canopy structure and the distribution of N within the canopy may provide information about the availability and ease of prehension of limpograss N under grazing conditions during the summer.

Properties of Ingested Plant Nitrogen

In addition to the functional properties of plant N in the sward canopy, there are also functional properties associated with plant N upon ingestion by the ruminant that govern how and when plant N is utilized. Nitrogen (protein) metabolism in the rumen (Russell and Hespell, 1981; Buttery and Lewis, 1982; Leng and Nolan, 1984), small intestine (Van't Klooster and Boekholt, 1972; Harrison et al., 1973), and large intestine (Dixon and Nolan, 1983 and 1986) have been intensively investigated and reviewed (Tamminga, 1979; Kennedy and Milligan, 1980; Krishnamoorthy et al., 1983; Van der Walt and Meyer, 1988). Here, an overview of ruminant N metabolism will be given as it relates to the concept of ingested plant N functionality and the utilization of ingested plant N from pasture.

Adding to the complexity of ruminant protein metabolism, and unique to the ruminant animal with regard to N metabolism, is the symbiotic relationship that exists between the host animal and the microflora in the rumen (Van Soest, 1982). Due to this symbiosis, multiple avenues are provided

through which dietary plant N (depending on form) can be utilized and converted into animal protein.

The distinction of plant N as being either non-protein (NPN) or true protein N is a major property of the functionality of ingested plant N. An important aspect of plant N when in the form of NPN is that it readily goes into solution in the rumen environment, is rapidly degraded to ammonia, and can be taken up by rumen bacteria and incorporated into microbial protein (Krishnamoorthy et al., 1983; Leng and Nolan, 1984). Uptake and incorporation depend upon a readily available energy source (Ernst et al., 1975; Johnson, 1976; Van Soest, 1982; Horn and McCollum, 1987; Bates et al., 1988). Thus, utilization of plant N (by the ruminant animal) in non-protein form is entirely dependent on rumen microbes (Van Soest, 1982). Rumen ammonia also may be absorbed across the rumen epithelium (Nolan and Macrae, 1976), converted to urea, and recycled (Cocimano and Leng, 1967), or excreted in the urine (Leng and Nolan, 1984).

Methods used to estimate forage NPN include hot water extraction (Goering and Van Soest, 1970) and direct measurement by colorimetry after isolation (Mangan and West, 1977). Composition of the soluble NPN fraction in plant material can be variable but is primarily composed of nitrate, glutamine, asparagine, and non-essential amino acids (Van Soest, 1982). There is little information in the literature regarding the amount of NPN in forages or its

composition. Nitrate-N may represent up to 20% of the total N content in crop plants (Hewitt et al., 1979).

Plant N that is in the form of true protein can be distinguished as either potentially digestible at some point in the digestive system, or as indigestible. The distinction between potentially digestible and indigestible N compounds can be considered as another functional property of ingested plant N. Although not discussed in the context of functionality, potentially digestible protein and indigestible dietary N compounds have received much attention in the literature in recent years (NRC, 1985).

Determination of N associated with acid detergent fiber (ADFN) arose from the interest in quantifying heat-damaged protein (Van Soest, 1962), and is currently being used to describe and quantify indigestible N compounds (Goering and Van Soest, 1970; Van Soest et al., 1982). Acid detergent fiber N, as a percentage of total N can vary greatly according to feedstuffs (Van Soest, 1982). Brown et al. (1988) reported ADFN values in the range of 10 to 20 g kg^{-1} (ADF basis) for four Cynodon varieties. These ADFN levels represented approximately 13% of total N in these tropical grasses. In another study (Brown et al., 1987), ADFN for 8-wk limpograss regrowth was reported to be 11 g N kg^{-1} ADF. Abdalla et al. (1988a) reported 3.6% of total N in bromegrass (Bromus inermis Leyss.) was associated with the ADF fraction.

Potentially digestible plant protein has been

characterized in a number of ways depending on the site of degradation within the ruminant digestive system (NRC, 1985) and the rate of degradation (Harrison et al., 1975; Van Soest, 1982). When potentially digestible protein is presented to the rumen, its accessibility to rumen microbes as well as its vulnerability to proteolysis are properties of the protein that initially determine whether or not ruminal microbial degradation will occur (Wallace and Kopechny, 1983) Additionally, structural characteristics of protein and the presence of disulfide bridges may have a major influence on degradability of proteins by rumen microorganisms (Mahadevan et al., 1980).

Recently, the concept of ruminally undegradable protein (RUP) has received much attention (NRC, 1985). Ruminally undegradable protein is feed protein that escapes or that is protected from rumen degradation. It is of particular importance in animals with high protein requirements such as lactating dairy cows (Waldo and Jorgensen, 1981; Erasmus et al., 1988) when protection of protein from rumen digestion is desirable because the biological or relative value of feed protein is higher than it would be if converted to microbial protein (Nugent et al., 1983; Leng and Nolan, 1984). The ability of plant protein to go readily into solution in the rumen environment has been a fairly good indicator of its degradability in the rumen (Crooker et al., 1978). This is

due to the fact that solubility of protein is often highly correlated with rumen digestibility (Stern and Satter, 1984).

Interest in measuring protein solubility has been spurred by the desire to equate solubility with digestibility so that solubility indices can be used to estimate escape protein (Pichard and Van Soest, 1977). Protein solubility assays have been used extensively to estimate protein digestibility in a variety of feedstuffs (Wohlt et al., 1976; Mahadevan et al., 1980; Wallace, 1983; Stern and Satter, 1984; Madsen and Hvelplund, 1985). Protein solubility assays have also been used to determine relative resistance to rumen proteolytic degradation of naturally occurring escape protein (Nugent et al., 1983) and proteins treated with formaldehyde (Ferguson et al., 1967; Kempton and Leng, 1979; Madsen et al., 1980), tannins (Driedger and Hatfield, 1972), and alcohols (Van Der Aar et al., 1982). Protein protection has also been achieved through heat and mechanical processing (Beever and Thompson, 1981).

Protein is extracted in solubility assays using various buffer solutions (Waldo and Goering, 1979; Mahadevan, et al., 1980; Krishnamoorthy, et al., 1983; Stern and Satter, 1984), saline solutions (Crooker et al., 1978), and isolated proteases (Wallace, 1983). Autoclaved rumen fluid (Crooker et al., 1978; Waldo and Goering, 1979; Mahadevan et al., 1980) and whole rumen liquor in both in vitro (Van Soest et al., 1982) and in situ (Stern and Satter, 1984) procedures are

also used. Extraction of protein is also accomplished with hot (Waldo and Goering, 1979; Goering and Van Soest, 1970) and cold water (Hargrasves et al., 1984) filtration.

Protein solubility is dependent upon the assay used (Crooker et al., 1978), making quantitative comparisons across solubility assays difficult. Although high correlations have been observed between protein solubility and digestibility, insolubility of protein does not necessarily imply indigestibility in the rumen (NRC, 1985). Likewise, some proteins that are highly soluble are poorly digested in the rumen (Nugent et al., 1983), particularly when complexed with tannins (Mangan et al., 1976). When protein solubility assays used for feed analysis are applied to forages or silages, the assay generally determines NPN, whereas protein solubility assays on natural protein feedstuffs may in some cases be over-estimating protein solubility (Pichard and Van Soest, 1977).

A major portion of the soluble protein in plant material is fraction 1 leaf protein, ribulose-1,5-diphosphate carboxylase (Nugent and Mangan, 1981). It is the major protein of chloroplasts and can account for up to 50% of the total leaf protein in temperate species (Brady, 1976). There is very little information in the literature related to the relative amounts of fraction 1 leaf protein in tropical grasses. It is not clear as to when fraction 1 leaf protein is isolated in the various solubility assays of forages but,

presumably, it would be accounted for in the rapidly degraded fraction (B_1) of Van Soest's classification scheme (Pichard and Van Soest, 1977).

It has been noted that most of the protein solubility assays in use rarely distinguish soluble true protein from NPN. Pichard and Van Soest (1977) developed a classification scheme for fractionating plant protein based on solubility and degradation rate. A water-soluble NPN fraction, comprised primarily of nitrate, ammonia, amines, and free amino acids with a degradation rate that is assumed to be infinite, has been designated as fraction A. True protein is divided into a rapidly degraded fraction (B_1) and a more slowly degraded fraction (B_2). Fraction C consists of the unavailable or indigestible protein that is associated with acid detergent residue and has a degradation rate constant that is considered to be zero. This classification scheme places more of an emphasis on the rate of protein degradation than on solubility, although it is implied that the B_1 fraction is probably highly soluble.

Another approach to classifying potentially digestible protein has been to identify protein that is associated with plant cell wall. Refluxing plant material in a neutral detergent solution followed by quantification of the residual fiber (NDF) has been used to estimate cell wall constituents (Goering and Van Soest, 1970). Analyzing the NDF fraction for N concentration provides a measure of the amount of plant

N associated with cell wall (NDFN; Abdalla et al., 1988a and 1988b). Neutral detergent is believed to dissolve cytoplasmic proteins, however, this may be incomplete at times (Richard and Van Soest, 1977) The composition of N associated with the NDF fraction has not been clearly defined. As was mentioned earlier, ADFN is thought to consist of indigestible N and accounts a portion of the N in NDF. The proportion of plant N associated with cell wall constituents (NDF) appears to be highly variable, particularly between temperate and tropical grasses. Abdalla et al. (1988b) reported that between 27 and 31% of the total N in four temperate grasses was associated with the NDF fraction. Brown et al. (1988) indicated that an average of 58% of the total N in four tropical grass species was associated with NDF.

How the association of N compounds with cell wall constituents affects their rate and extent of digestion is not known and has received little attention. Lang and Nolan (1984) have noted that degradation of particulate proteins may depend in part on physical characteristics of feed particles themselves, which may affect accessibility of proteins to proteolytic attack. This may be of particular significance with tropical grasses due to the relatively large proportion of total N that is apparently associated with the plant cell wall constituents.

In the context of functionality of potentially digestible plant protein upon ingestion, it is clear that physicochemical and structural characteristics of plant N will affect where and to what extent plant N is utilized by the ruminant animal. Characterizing protein in terms of solubility alone, does not provide information about the properties of plant N that affect its utilization by ruminants. This is of particular significance for tropical grasses, in which a relatively high percentage of plant N is insoluble and associated with NDF. Under grazing conditions, where the animal is totally dependent on forage for meeting its protein requirements, it may be more informative to characterize and describe plant N functional properties in terms of N form (e.g., NPN versus true protein) as well as association of N with structural constituents (i.e., NDF and ADF) of the plant material.

Increasing the Dietary Crude Protein Intake of Ruminants

Reports of low CP concentration in limpograss have led to speculation that a limitation of dietary CP on limpograss pasture contributes to the poor performance of grazing steers during the summer through early fall. Increasing CP intake of grazing steers during this time may help to alleviate the slump in animal performance. There are several management

approaches to increasing the dietary CP intake of grazing steers.

The positive response to fertilizer N application of yield and CP concentration of forage grasses has been well documented (Sieser, 1964, Power, 1986). Increasing the CP concentration of a grass pasture can increase the dietary CP intake of grazing cattle.

Inclusion of a legume in a grass sward has been suggested as an economical approach to overcoming a protein deficiency in grass pastures (Minson, 1980). This has been particularly successful with ware-season perennial grasses grown in the southeastern United States (Evans, 1985; Sollenberger et al., 1987b). Seeding aeschynomene (Aeschynomene americana L.) into limpograss pastures has been effective in increasing overall herbage CP concentration and improving steer ADG, particularly during the summer slump period (Rusland et al., 1988). Similar benefits have been reported with temperate grass pastures as well (Ellis et al., 1983). In addition to legumes being used in association with grass pastures, legumes have also been used as supplemental pasture. Schnaichal et al. (1988a and 1988b) reported on the use of Stylosanthes capitata pasture as a supplement to cattle grazing native savanna during the summer.

Another approach to increasing dietary CP intake of grazing animals is to augment the animal's diet through feeding of a high-protein supplement. Many different types

of protein have been used as sole supplements or in combinations (Peterson et al., 1985). There is currently much interest in the use of RUP for meeting protein requirements of ruminants (NRC, 1985), particularly for animals with a high production potential and protein requirement such as dairy cows (Wohlt and Clark, 1978). Examples of escape protein supplements include corn gluten meal, protected casein, and bloodmeal (Peterson et al., 1985; Kempton and Leng ,1979), to name just a few. Numerous comparisons have been made between ruminally degradable and undegradable protein supplements relative to their effectiveness in improving animal gain and feed intake (Redman et al., 1980). Here, a discussion of NPN supplements will be given with particular attention to urea as a source of protein for growing steers.

With respect to meeting the protein requirements of ruminants, Orskov (1982) emphasized the importance of recognizing a two-stage approach that includes providing nutrients for the microorganisms in the rumen as well as for the host animal. Ammonia is the primary form of N utilized by rumen bacteria in the synthesis of protein (Van Soest, 1982), although, other N compounds (e.g., amino acids) can be utilized by certain rumen organisms (Russell et al., 1983). Due to a requirement for NH_3 by rumen organisms, low digestibility of certain feeds and forages has been attributed to NH_3 deficiencies in the rumen (El-Shazly et

al., 1961). Satter and Slyter (1974) suggested that NPN supplementation was justified when rumen NH_3 concentration was less than 5.0 mg NH_3-N l^{-1} rumen fluid.

Even though the use of NPN supplementation has often been based on insufficient rumen NH_3 concentrations, there is disagreement as to whether NH_3 is a limiting factor (Peterson, 1987) in ruminant microbial nutrition and why responses to supplemental NPN are observed. Heapell and Bryant (1979) hypothesized that improved DM digestibility with NPN supplementation is due to an increase in rumen pH resulting from the formation of ammonium bicarbonate following an elevation in rumen NH_3 concentration. Egan and Doyle (1985) suggested that the stimulatory effects of urea upon intake were associated with the provision of additional microbial protein for digestion in the lower tract, rather than changes in the rate or extent of OM digestibility in the rumen.

Due to the long history of NPN supplement use in ruminant diets (Kwan et al., 1977) and its general acceptance as an effective approach to increasing dietary CP intake, current disagreements in the mechanisms of NPN responses have not impeded its use or application. Variable responses to urea supplementation have been reported in the literature. Increases in feed intake (Campling et al., 1962; Hemsley and Moir, 1963; Kempton and Leng, 1979) and digestibility (Coombe and Tribe, 1963; McAllen and Griffith, 1987) due to urea

supplementation have been reported. Others have reported little benefit from urea supplementation with cattle grazing low-quality grass pasture (Williams et al., 1967; Smith, 1984) or winter range (Ruth and Totusek, 1976; Clanton, 1978). Lee et al. (1987) recently reported that animal gains of 2-yr-old Hereford steers on a basal diet of low-quality (4.3 g N kg^{-1} DM) pasture hay were higher with a pelleted protein meal than with urea when diets were isonitrogenous. When compared to the effects of protected protein, supplemental urea resulted in a similar increase in oat (Avena sativa L.) chaff (5.7 g N kg^{-1} DM) intake (Redman et al., 1980). Hunter and Siebert (1980) reported that cattle supplemented with protein meals gave more consistent responses in intake of mature spear grass (Heteropogon contortus) than when urea was administered via continuous infusion to the rumen. In a study with Israeli-Friesian dairy cows fed a vetch (Vicia villosa Roth)-oats hay, Bruckental et al. (1986) reported that urea (as urea phosphate) tended to improve total milk and milk protein yields as well as liveweight gain.

It would appear from the literature that the effectiveness of protein supplementation (as NPN and urea, in particular) in improving animal performance is dependent on a number of factors. Of primary importance is the relationship between the occurrence of a readily fermentable carbohydrate source and microbial-available N (Ernst et al., 1975; Smith,

1979; Oldham and Smith, 1982; Horn and McCollum, 1987). In a study with mature (8-wk regrowth) limpograss hay (42 g CP kg^{-1} DM) fed to cattle, Brown et al. (1987) reported that ammoniation increased apparent digestion coefficients of OM, NDF, ADF, and hemicellulose, and animal gain compared to nontreated forage plus urea or molasses-urea. In a similar study with 14-wk regrowth limpograss hay (28 g CP kg^{-1} DM) fed to lambs, Bates et al. (1988) suggested that the major factor limiting the effectiveness of a molasses-urea supplement was the imbalance between ruminally available N and digestible OM (DOM) available to fuel microbial protein synthesis in the rumen. Hogan and Weston (1981) have suggested that a N limitation to microbial protein synthesis appears likely when the ratio of DOM to CP in the diet exceeds 10. Hume et al. (1970) found no further increase in the flow of microbial protein to the omasum when the DOM to CP ratio in purified cellulose-based diets fed to sheep was lowered from 7.4 to 4.2 by the addition of urea. Egan and Doyle (1985) reported that the maximum intake of OM was achieved when the DOM to CP ratio in the diet was reduced, by infusing urea, from 10.4 to 8.4. Thus, the effectiveness of urea as a dietary N source is dependent on both a source of readily fermentable carbohydrate and the ratio of total dietary DOM to CP.

CHAPTER III
PROTEIN SUPPLEMENTATION OF STEERS
GRAZING LIMPOGRASS PASTURE

Introduction

'Floralta' limpograss [Hemarthria altissima (Poir.) Stapf et C.E. Hubb.] is gaining popularity for use in improved pasture-livestock production systems in Florida due to its high-yielding ability and persistance under grazing (Quesenberry et al., 1984). However, Floralta limpograss (LG) herbage tends to be marginal in terms of crude protein (CP) concentration for growing steers (Bos spp.) (Soilenberger et al., 1987b; Rusland et al., 1988).

The term "summer slump" has been used to describe a period of time when a decline is observed in animal performance of cattle grazing summer pasture. In Florida, this slump in performance is usually observed sometime between late July through mid-September on tropical grass pastures such as LG. Reports of low CP concentration in LG have led to speculation that a limitation of dietary CP on LG pasture contributes to the low performance of grazing steers during the summer and early fall.

Inclusion of a legume in a grass sward has been suggested as an economical approach to overcoming a protein

deficiency in grass pastures (Minson, 1980). Seeding aeschynomene (Aeschynomene americana L.) into LG pastures has been effective in increasing overall herbage CP concentration and improving steer average daily gain (ADG), particularly during the summer slump period (Rueland et al., 1988).

Protein supplementation has been used in many livestock production systems to increase overall dietary CP intake. Supplementation of low-quality forage (low CP concentration) with non-protein N (NPN) such as urea (Raymond, 1969) has been reported to increase rumen ammonia concentration (Lee et al., 1987) and OM intake (Egan and Doyle, 1985; Redman et al., 1980; and Kempton and Leng, 1979). Others have reported little or no response to NPN supplementation of low-quality roughages (Rush and Totusek, 1976; Williams et al., 1967). It is hypothesized that limited protein supplementation (as NPN) of steers on LG pasture will improve DM intake and animal performance during the summer slump period.

Objectives of this study were to a) determine the effects of protein supplementation on animal performance of steers grazing LG pasture during mid-summer to early fall and b) compare animal performance of steers receiving protein supplementation on LG pasture to those receiving no supplement and grazing a LG/aeschynomene association.

Materials and Methods

The experiment was conducted in 1987 and 1988 at the Forage Evaluation Field Laboratory of the Beef Research Unit north of Gainesville, Florida. Floralta LG pastures used in this study were 0.5 ha and were established between 1980 and 1983. All pastures were managed similarly with respect to fertilization and grazing prior to this experiment. The predominant soil series on the experimental site were Pomona and Smyrna sands (sandy, siliceous, hyperthermic Ultic Haplaquods). These soils are moderately to poorly drained and are of low natural fertility.

Mean soil pH and Mehlich I extractable (mg kg^{-1}) P, K, and Mg at the beginning of each year were 5.9 and 18, 29, and 94, respectively, in 1987, and 5.7 and 20, 24, and 103 in 1988. Fertilization rates and schedules were similar for all LG pastures within each year. Dolomitic limestone was applied to individual pastures in the spring of each year only when soil tests indicated pH levels below 5.5. Pastures overseeded with aeschynomene did not receive fertilizer N. Phosphorous (90 kg P_2O_5 ha^{-1}) and K (90 kg K_2O ha^{-1}) were broadcast applied on 17 Apr. 1987 and 22 Apr. 1988. A micronutrient mixture supplying 0.8 kg B, 0.8 kg Cu, 3.8 kg Fe, 1.5 kg Mn, 0.04 kg Mo, and 1.4 kg Zn ha^{-1} was applied in both years at the time of P and K application. The LG pastures received 4 equal split applications of N (as NH_4NO_3)

at annual rates of 120 kg ha^{-1} in both years. The first N application each year was made in conjunction with P and K fertilization. Subsequent N applications were made immediately following each grazing cycle except the last of the season.

In spring each year, LG pastures were divided into six paddocks of equal size (0.083 ha) with electric fencing. A 42-d rotational grazing system was used such that grazing periods on each paddock were 7 d followed by a 35-d rest period. The period of the grazing season of primary interest in this experiment was from mid-summer through early fall (i.e., July through September). In 1987, rotational grazing was initiated on LG pastures beginning the last week of May. This allowed for staging of pasture growth among paddocks within each pasture prior to commencement of the grazing experiment on 9 July. Steers previously assigned as testers to respective pastures for the grazing study were used during the pre-experimental period to a) accustom the animals to grazing LG and b) acclimate the steers to rotational grazing. Put-and-take animals were used as needed during both initial spring grazing and the experimental period so that the residual stubble height was approximately 20 cm on each paddock at the end of 7 d grazing. The grazing season was 84 d ending on 1 Oct. 1987.

In 1988, pre-staging of the rotational grazing system was not possible due to slow pasture growth during late

spring and early summer. This was due to abnormally low rainfall from April through July (Table 3.1). Mean LG pasture canopy height at the initiation of the grazing study in 1988 was 37 cm compared to 63 cm in 1987. Grazing was initiated on 7 July 1988 with tester animals assigned to respective treatment pastures. Testers were given access to paddocks 1 and 2 on each pasture on 7 July and the experiment was initiated on paddock 3 the following week (14 July). Grazing continued for 84 d and ended on 6 Oct. 1988.

Establishment of aeschynomene in the LG-aeschynomene (LA) pastures was done in 2 stages in both years as described by Rusland et al. (1988). They reported that planting aeschynomene in all paddocks at the same time resulted in excessively tall and stemmy legume herbage in the last few paddocks by the time that they were grazed under a rotational system. To avoid this problem, paddocks 1 through 3 were planted in early June and paddocks 4 through 6 were seeded 3 wk later. Timing of the legume establishment was scheduled so that initiation of grazing on LA pastures would coincide with that on LG pastures.

Irrigation was used during the establishment period in 1987 only when moisture stress conditions were evident and to insure successful establishment. In 1988, establishment of aeschynomene was hampered by severe drought that occurred in May and June and was unsuccessful on one of the LA pasture replicates. This pasture was excluded from the study.

Table 3.1. Monthly rainfall totals (March to October) in 1987 and 1988 at the Beef Research Unit, Gainesville, Florida.

Month	Year 1987	Year 1988	70-yr mean
	mm		
March	223	195	93
April	12	26	74
May	97	53	106
June	47	57	167
July	82	60	176
August	139	356	204
September	51	245	143
October	6	23	59
Total	657	1015	1022

Following establishment of the eastchynomene, LA pastures were subdivided into 6 paddocks identical to the LG pastures. The experimental grazing period was initiated when the eastchynomene in paddock 1 attained a height of approximately 30 cm. This occurred by 8 July 1987, but grazing of LA pastures did not begin until 10 Aug. 1988, allowing for only a 63-d grazing season compared to 84 d of grazing on the LG pastures in the same year. Limpograss-eastchynomene pastures were grazed to a 15-cm residual stubble height for reasons discussed by Rueland et al. (1988).

Tester animals assigned to each pasture in 1987 were selected from two breed groups of yearling steers. One group was crossbred (50% Hereford, 25% Brahman, 12.5% Angus, and 12.5% Brown Swiss) and the other purebred Angus. The steers had been over-wintered on sorghum [Sorghum bicolor (L.) Moench] silage and each fed 1.0 kg corn (Zea mays L.) and 0.45 kg soybean [Glycine max (L.) Merr.] meal d^{-1} and free-choice molasses so that steer ADG was between 0.25 and 0.5 kg. One steer from each breed group was assigned as a tester to each pasture providing a base stocking rate of four animals ha^{-1} (Queenberry et al., 1984). Tester steers were approximately 18 months old and weighed an average of 315 kg at the start of the grazing study.

In 1988, tester animals used were all of the same crossbred lineage as in 1987 with 2 steers assigned as testers to each pasture. The tester animals for the 1988

study were over-wintered in a similar manner as in 1987, but LG haylage was used instead of sorghum silage. Tester animals were approximately 18 months old in 1988. The average weight of testers assigned to LG pastures at the start of the grazing study (14 July) was 362 kg. Testers assigned to each LA pasture averaged 375 kg when grazing was initiated on these pastures (4 August). Prior to the commencement of grazing on the LA pastures, the testers were maintained on LG and bahiagrass (Paspalum notatum Flugge) pasture. All tester animals were implanted with Raigro (36 mg zeranol) on 20 July 1987 and 4 July 1988. Water and a salt-based trace mineral mix was supplied free-choice at all times during the grazing study in both years.

Pasture treatments were no supplementation on LG pasture (NP), low protein supplementation on LG pasture (LO), high protein supplementation on LG pasture (HI), and LA. The objective in supplementing grazing steers for the LO and HI treatments was to increase total dietary CP intake to two different levels above that of steers grazing LO pastures alone. Mean CP, organic matter (OM), and in vitro digestible organic matter (IVDOM) concentrations of the LG diet during midsummer to early fall were estimated to be 80 g kg^{-1} DM, 950 g kg^{-1} DM, and 600 g kg^{-1} OM, respectively. These values were selected based on the data of Rusland et al. (1988) and were used for formulating the LO and HI protein supplements.

The two levels (treatments) of protein supplementation, LO and HI, were formulated to provide approximate total dietary CP concentrations of 90 g and 120 g CP kg^{-1} OM consumed. Calculations were also based on a 350-kg animal with an average daily OM intake of 2.2% of body weight; implying an OM intake of 7.32 kg d^{-1} on LG pasture. Corn meal (80 g CP kg^{-1} and 800 g DOM kg^{-1}) and feed grade urea (419 g N kg^{-1}) were used in formulating the protein supplements. Urea was chosen as the primary source of protein so that the supplement treatments could be made isocaloric and avoid bias attributable to protein quality. The maximum CP concentration in the supplement (HI) was set at 500 g CP kg^{-1} so as to ensure palatability and acceptance of the supplement by the animals. The LO supplement was isocaloric to the HI and contained a lower total concentration of CP (210 g kg^{-1}). The two supplements were designed to be isocaloric so that if a higher response in animal performance was obtained on the HI treatment compared to LO, it would be indicative of a response to additional N (as urea). The following equations were used in the derivation of the supplement formulations:

Organic matter intake (OMI) of NP was calculated as:

$$X = W * I_f * OM_f \qquad \text{[Eq.1]}$$

where:

X = OMI of unsupplemented LG forage
W = mean animal body weight (350 kg)
I_f = intake of forage (.022 kg DM (kg BW)$^{-1}$
OM_f = forage OM concentration (.950 kg OM kg^{-1} DM)

such that:

$$X = 7.32 \text{ kg OM d}^{-1}$$

The amount of corn and urea as fractions of total supplement DM are described by the following equations:

$$\text{corn supplement} = P * Y \quad \text{[Eq. 2a]}$$

$$\text{urea supplement} = (1-P) * Y \quad \text{[Eq. 2b]}$$

where:

Y = total daily supplement (kg DM)
P = fraction of total supplement that is corn
1-P = fraction of total supplement that is urea

The CP concentration of the HI supplement was set at 500 g CP kg^{-1}. The proportions of corn and urea needed to meet this level were determined with the following equation:

$$CP_s = [CP_c * P] + [CP_u * (1-P)] \quad \text{[Eq. 3]}$$

where:

CP_s = CP concentration of total supplement (500 g kg^{-1})
CP_c = CP concentration of corn (80 g kg^{-1})
CP_u = CP concentration of urea (2620 g kg^{-1})

such that:

$$P = 0.835$$

and

$$1 - P = 0.165$$

Substitution of forage by supplement was estimated to be 50% of corn OM intake (Golding et al., 1976) so that OMI of forage when supplemented is described by the following:

$$\text{forage OMI when supplemented} = X - T*P*Y \quad \text{[Eq. 4]}$$

where:

X = (from [Eq. 1])
T = substitution rate of forage OM by supplement OM (0.5)
P = (from [Eq. 3])
Y = (from [Eq. 2])

Therefore, daily forage CP intake [CPI_f] when supplemented is described as:

$$CPI_f \text{ when supplemented} = CP_f[X - T*P*Y) \quad \text{[Eq. 5]}$$

where:

CP_f = CP concentration of forage

and the CP content of the supplement is described as:

$$\text{kg CP in supplement} = CP_s*Y \quad \text{[Eq. 6]}$$

Total dietary CP concentration can be described by dividing the sum of equations [3] and [4] by the sum of equations [5] and [6] as follows:

$$\frac{\text{Total CP intake}}{\text{Total OM intake}} = \frac{CP_s*Y + [CP_f(X - T*P*Y)]}{P*Y + X - T*P*Y} \quad \text{[Eq. 7]}$$

Setting desired total dietary CP concentration at 120 g kg^{-1} and OMI of LG when unsupplemented (X) at 7.32, total kg of supplement [Y] for HI equals:

$$0.12 = \frac{0.5Y + [0.08(7.32 - 0.5(0.835Y))]}{0.835Y + [7.32 - (0.835Y)]}$$

such that:

$$Y = 0.703 \text{ kg}$$

Inserting 0.703 for Y in equations [2a] and [2b], the

amount of corn and urea in the HI supplement is 0.587 and 0.116 kg, respectively.

Total OMI excluding urea equals the sum of Eq. [4] and Eq. [2a]:

$$\text{Total OMI} = 0.587 + 7.32 - 0.5(0.587) \quad \text{[Eq. 8]}$$

The amount (kg) of urea used in formulating the LO supplement is determined by first calculating total CP intake (kg d^{-1}) when total dietary CP concentration is set at 90 g kg^{-1} and using total OMI at 7.61 kg d^{-1} (from Eq. [8]).

$$\text{Total CP intake} = 0.09\ [0.587 + 7.32 - 0.5(0.587)] \quad \text{[Eq. 9]}$$

such that total CP intake for the LO supplement diet is 0.685 kg d^{-1}. The amount of CP (kg) contributed by the LO supplement is determined by subtracting the CP intake of forage (0.562 kg, Eq. [5]) from total CP intake (0.685 kg, Eq. [9]), such that:

$$\text{LO supplement CP} = 0.123 \text{ kg}$$

The amount of urea in the LO supplement (U) is calculated as:

$$U * CP_U = 0.123 - (CP_C * FY)$$

such that:

$$U = 0.029 \text{ kg}$$

The amount of corn and urea in the LO supplement is 0.587 and 0.029 kg, respectively.

The S to N ratio in both the LO and HI supplements was adjusted to 1:12 (Elliot and Armstrong, 1982) by adding a commercial mineral product that contained 223 g S kg^{-1}. The

final formulations (expressed as kg of corn, urea and mineral in total supplement DM fed per day) for the LO and SI supplements were 0.587, 0.029, and 0.007, and 0.587, 0.116, and 0.021, respectively.

Steers (all testers, and put-and-take animals when utilized) were weighed every 21 d following a 16-h fast on dry lots. Blood samples were collected (10 ml) from the jugular vein of tester animals at the time of weighing. The plasma was separated by centrifugation, frozen, and subsequently analyzed for urea N (BUN). Blood urea N was determined by automated colorimetric analysis (Marsh et al., 1965). Average daily gains reported are based on tester animals. Steer days ha^{-1} was determined by calculating the 100 kg liveweight days ha^{-1} of both tester and put-and-take animals and dividing by the mean 100 kg liveweight of the testers. Carrying capacity was expressed as kg of animal (tester and put-and-take) liveweight ha^{-1} d^{-1}. Gain ha^{-1} is calculated as the product of ADG and steer days ha^{-1}.

Pre- and post-graze pasture samples were taken every 21 d, alternately on paddocks 1 and 4 in each pasture in 1987 and paddocks 2 and 5 in 1988, during the experimental period. Four sample sites (0.5 m^2) were selected in the respective paddocks to represent mean forage availability and pasture condition at pre- and post-graze. Samples were clipped to a 5-cm height and separated into LG, weed, dead, and arachyhomena (when applicable) components. All botanical

components were forced-air dried at 60°C for 48 h. Dried samples were then weighed and dead material discarded. In 1988, the same pre-graze sampling procedure was used. The DM data from pre- and post-graze samples are used for estimating mean seasonal herbage accumulation (HA) and botanical composition within pasture types. Herbage accumulation was calculated as mean pre-graze green herbage mass for sampling dates 1 and 2 plus mean pre-graze green herbage mass for sampling dates 3 and 4 minus mean post-graze green herbage mass for sampling dates 1 and 2 and adjusted for growth during the grazing periods.

Hand-plucked samples were obtained at the time of pre-graze sampling by collecting herbage at approximately 20 randomly selected sites within the paddock. The hand-plucked herbage was severed at the target post-graze residue stubble height (20 cm and 15 cm for LG and LA pastures). Hand-plucked samples were dried and analyzed for N and IVDOM. A modified aluminum block digestion procedure (Gallaher et al., 1975) and semi-automated colorimetry (Hambleton, 1977) were used for all N determinations, and CP concentration was calculated as N X 6.25 on a DM basis. In vitro digestible organic matter concentration was determined using a modified two-stage digestion procedure (Moore and Mott, 1974).

The experimental design was completely randomized with two replications. Seasonal data were analyzed by analysis of variance using SAS General Linear Models procedures

Treatment mean comparisons, when appropriate ($P \leq 0.10$), were done with preplanned contrasts. Of major interest were the comparisons between no supplementation and supplementation (NP vs. LO + HI), low protein and high protein supplementation (LO vs. HI), and the grass-legume association and supplementation (LA vs. LO + HI).

Repeated measures (sampling period) analysis of variance procedures were used for analysis of by period data within a year. Statistics were based on the univariate approach with degrees of freedom correction. Due to unsuccessful establishment of aeschynomene in one of the replicates in 1988, LA responses reported for 1988 are of a single replicate and period data are presented for comparison purposes only. The LA treatment was not included in the by period model for 1988. Mean comparisons for treatment effects when appropriate ($P \leq 0.10$) were made using the preplanned single degree of freedom contrasts described above. Between period comparisons, when appropriate, were also done by preplanned contrasts. These contrasts were based on comparing the period of the grazing season in which ADG was lowest with each of the others within a year. Crude protein and IVDOM data for LG and LA pasture hand-plucked samples were analyzed in a similar manner with mean comparisons conducted when appropriate ($P \leq 0.05$).

Results

Seasonal Animal Performance Responses

There was no TRT by YEAR interaction for seasonal (84 d) ADG (Table 3.2) but there was a main effect of TRT (P = 0.024). Seasonal ADG was not different among LO (0.53 kg d^{-1}), HI (0.59), and LA (0.52) but all were higher than NP (0.29) (Table 3.3). Mean ADG was higher (P = 0.069, Table 3.2) in 1987 (0.53 kg d^{-1}) than in 1988 (0.44).

As with ADG, seasonal CC differences were observed (Table 3.2) due to TRT (P = 0.003) and YEAR (P = 0.003) but there was no interaction. Mean CC (Table 3.3) was higher in 1988 (2300 kg LW ha^{-1} d^{-1}) than in 1987 (1960). Carrying capacity was similar for pastures without supplementation (NP) to those with supplementation (LO and HI) (Table 3.3), but CC was lower for HI (2130 kg LW ha^{-1} d^{-1}) when compared to LO (2380). Carrying capacity for LA (1620) was lower than for the other three treatments.

Steer gain ha^{-1} tended to be higher (P = 0.103) in 1987 (253 kg ha^{-1}) than in 1988 (204) (Tables 3.2 and 3.4). Mean gain ha^{-1} (over years) for the supplement treatments (LO and HI) was not different and averaged 288 kg ha^{-1} (Table 3.4). Steer gain ha^{-1} on unsupplemented LG pasture (NP; 168 kg ha^{-1}) was similar to that on LA (169) but both were lower than that on LO and HI

Table 3.2. Levels of probability for differences in seasonal steer average daily gain (ADG), carrying capacity (CC), blood urea nitrogen (BUN), animal gain ha^{-1} (GAIN), and herbage accumulation (HA) due to treatment (TRT), year (YEAR), and their interaction.

	Response Variable				
Effect	ADG	CC	BUN	GAIN	HA
YEAR	0.069	0.003	0.467	0.103	0.329
TRT	0.024	0.003	0.057	0.040	0.084
YEAR*TRT	0.851	0.945	0.577	0.658	0.214

Table 3-3. Least squares means for seasonal steer average daily gain (ADG) and carrying capacity (CC) as affected by pasture treatment (TRT) in 1987 and 1988.

	ADG			CC		
	Year			Year		
TRT[+]	1987	1988	Mean	1987	1988	Mean
	kg			-- kg LW ha^{-1} d^{-1}‡ --		
NP	0.36	0.23	0.29	2150	2600	2380
LO	0.53	0.53	0.53	2230	2520	2380
HI	0.64	0.54	0.59	1990	2280	2130
LA[§]	0.60	0.44	0.52	1460	1790	1620
Mean	0.53	0.44		1960	2300	
SE¶#	0.050¶		0.078#	0.41¶		130#

Results of significance tests for planned comparisons between treatment means

Planned comparison		
NP vs. LO + HI	**	NS
LO vs. HI	NS	*
LA vs. LO + HI	NS	**

*, **, NS $P \leq 0.05$ and 0.01, and $P > 0.10$, respectively.

+ NP, LO, and HI are no, low, and high protein supplementation of limpograss pasture. LA is a limpograss-aeschynomene association.

‡ Carrying capacity is expressed as kilograms of liveweight per hectare per day.

§ There were 63 d of grazing for LA in 1988, all other treatment means within a year are based on an 84-d grazing season.

¶, # Largest standard errors for year and treatment means, respectively.

Table 3.4. Least squares means for animal gain ha^{-1} (GAIN) and blood urea nitrogen (BUN) as affected by pasture treatment (TRT) in 1987 and 1988.

	GAIN			BUN		
	Year			Year		
TRT†	1987	1988	Mean	1987	1988	Mean
	----- kg ha^{-1} -----			---- mg 100 ml^{-1} ----		
NP	197	138	168	8.2	5.8	8.0
LO	284	294	289	6.8	9.6	8.2
HI	318	260	288	11.9	10.9	11.4
LA‡	214	124	169	10.4	12.0	11.0
Mean	253	204				
SE§¶	21.1§		32.7¶			1.08¶

Results of significance tests for planned comparisons between treatment means

Planned comparison		
NP vs. LO + HI	*	*
LO vs. HI	NS	++
LA vs. LO + HI	*	NS

*, ++, NS $P \leq 0.05$ and 0.10, and $P > 0.10$, respectively.

† NP, LO, and HI are no, low, and high protein supplementation of limpograss pasture. LA is a limpograss-aeschynomene association.

‡ There were 63 d of grazing for LA in 1988, all other treatment means within a year are based on an 84-d grazing season.

§, ¶ Largest standard errors for year and treatment means, respectively.

There was no TRT by YEAR interaction (P = 0.577) for mean seasonal BUN (Table 3.2), nor did BUN differ by year (P = 0.467). There was a TRT effect (P = 0.057) on seasonal BUN such that the average of HI (11.4 mg 100 ml^{-1}) and LO (8.2) was higher than HP (6.0) (Table 3.4). Blood urea nitrogen for HI was higher than that for LO, but mean BUN on the supplemented treatments and on LA (11.0) were not different.

There was no PER by YEAR interaction for HA (P = 0.214, Table 3.2). Herbage accumulation did not differ between years and averaged 10150 kg DM ha^{-1} for 1987 and 8920 kg DM for 1988 (data not shown). There was a main effect of TRT (P = 0.084), and HA (kg DM) was lower for LA (5700) than for the LG pastures (10930) (data not shown).

Pre-graze herbage mass was not different among LG pastures and averaged 7030 kg of green herbage ha^{-1} (data not shown). However, pre-graze herbage mass for LA pastures was lower than for LG pastures. There were also no differences observed in post-graze herbage mass among LG pastures but post-graze mass for LA was lower than LG.

Animal Performance Responses by Period

There was no treatment (TRT) by period (PER) interaction for ADG in 1987 or 1988 (Table 3.5). There was no effect of treatment on ADG, when averaged over periods in either year (P = 0.215 in 1987 and P = 0.166 in 1988). Average daily

Table 3.5. Levels of probability for differences in steer average daily gain (ADG), carrying capacity (CC), and blood urea nitrogen (BUN) due to treatment (TRT), period (PER), and their interaction in 1987 and 1988.

	Response Variable		
Effect	ADG	CC	BUN
		1987	
TRT	0.215	0.048	0.093
PER	0.008	0.054	0.004
TRT*PER	0.487	0.046	0.245
		1988	
TRT	0.166	0.157	0.250
PER	0.001	***	0.008
TRT*PER	0.450	0.077	0.870

*** P < 0.001.

gain tended to be higher, particularly during the last 21-d grazing period in each year, for steers supplemented with corn-urea (LO and HI treatments) and for steers grazing LA pasture than for those grazing LG alone (NP) (Tables 3.6 and 3.7). There was a period effect on ADG in 1987 ($P = 0.008$) and in 1988 ($P = 0.001$). Among TRT, ADG for the second period (20 August, 0.25 kg d^{-1}) in 1987 was lower than for each of the other three periods (Table 3.6). In 1988, among TRT ADG for the third period (15 September, -0.03 kg d^{-1}) was lower than that of each of the other periods (Table 3.7). Data for LA in 1988 (Table 3.7, single replicate) indicated ADG was highest for 15 September (1.02 kg d^{-1}).

There was a TRT by PER interaction for CC in 1987 ($P = 0.046$, Table 3.5) that was primarily due to the low CC on LA pasture during the first (880 kg LW ha^{-1} d^{-1}) and second (1770) periods relative to CC for treatments on LG pasture (Table 3.8). Within TRT CC in 1987 was consistently lower during the fourth period (1 October) compared to the second period (20 August) for all treatments. There was also a TRT by PER interaction ($P = 0.077$) in 1988 among the LG pasture treatments (Table 3.5), with TRT differences being greatest within the first (30 July) and last (1 October) period (Table 3.9). Single degree of freedom contrasts showed higher ($P \leq 0.05$) CC for NP (2860 kg LW ha^{-1} d^{-1}) than for the average of LO and HI (2340) during the first period; however, the reverse relationship was observed in the last period. In

Table 3.6. Steer average daily gain (ADG) as affected by period and pasture treatment in 1987.

Treatment‡	Period†			
	30 July	20 Aug	10 Sept.	1 Oct.
	---------- kg ----------			
NF	0.21	0.20	0.52	0.45
LO	0.72	0.20	0.40	0.80
HI	0.86	0.23	0.70	0.78
LA	0.50	0.37	0.51	0.99
Mean	0.57§	0.25	0.54§	0.76¶
(0.084)#				

† Means within a period represent the response during the previous 21 d.

‡ NF, LO, and HI are no, low, and high protein supplementation of limpograss pasture. LA is a limpograss-aeschynomene association.

§,¶ Period mean over treatments differed from that of 20 August at $P \leq 0.01$ and $P \leq 0.10$, respectively.

Standard error for period means.

Table 3.7 Steer average daily gain (ADG) as affected by period and pasture treatment in 1988.

Treatment‡	Period+			
	4 Aug.	25 Aug.	15 Sept.	6 Oct.
	kg			
NP	0.59	0.29	-0.43	0.47
LO	0.67	0.50	0.16	0.79
HI	0.60	0.44	0.19	0.91
Mean (0.108)¶	0.62§	0.41§	-0.03	0.72§
LA#	-	0.20	1.02	0.11

+ Means within a period represent the response during the previous 21 d.
‡ NP, LO, and HI are no, low, and high protein supplementation of limpograss pasture. LA is a limpograss-aeschynomene association.
§ Period mean over treatments differed from that of 15 September ($P \leq 0.01$).
¶ Standard error for period means.
# Data are for a single replicate and are presented for comparison purposes, only.

Table 3.8. Carrying capacity (CC) as affected by period and pasture treatment in 1987.

Treatment‡	Period+ 30 July	20 Aug.	10 Sept.	1 Oct
	kg LW ha^{-1} d^{-1}§			
NP	1940	1920	1970	1570¶
LO	2770	2090	2020	1570¶
HI	1880	1920	1770	1520¶
LA	880#	1770	1660	1430¶
(198)++				

Results of significance tests for planned comparisons

Planned comparison				
NP vs. LO + HI	NS	*	NS	NS
LO vs. HI	NS	**	NS	NS
LA vs. LO + HI	*	***	NS	NS

*,**,***,NS P ≤ 0.05, 0.01, and 0.001, and P > 0.10, respectively.

\+ Means within a period represent the response during the previous 21 d.

‡ NP, LO, and HI are no, low, and high protein supplementation of limpograss pasture. LA is a limpograss-aeschynomene association.

§ Carrying capacity is expressed as kilograms of liveweight per hectare per day.

¶,# Period mean within treatments differed from that of 20 August at P ≤ 0.01 and P ≤ 0.10, respectively.

++ Standard error for period by treatment means.

Table 3 9. Carrying capacity (CC) as affected by period and pasture treatment in 1988.

Treatment‡	Period†			
	4 Aug.	25 Aug	15 Sept	6 Oct.
	kg LW ha^{-1} d^{-1}§			
NP	2a60	3380¶	2650	1480#
LO	2720	2970	2780	1670#
HI	1970#	2740	2730	1670#
(160)++				
LA‡‡	-	1040	790	820

Results of significance tests for planned comparisons

Planned comparison				
NP vs. LO + HI	*	NS	NS	*
LO vs. HI	**	NS	NS	NS

*,**,NS P ≤ 0.05 and 0.01, and P > 0.10, respectively.

† Means within a period represent the response during the previous 21 d.

‡ NP, LO, and HI are no, low, and high protein supplementation of limpograss pasture. LA is a limpograss-aeschynomene association.

§ Carrying capacity is expressed as kilograms of liveweight per hectare per day.

¶,# Period mean within treatments differed from that of 15 September at P ≤ 0.10 and P ≤ 0.01, respectively.

++ Standard error for period by treatment means.

‡‡ Data are for a single replicate and are presented for comparison purposes, only.

1988, CC within each TRT was lower during the last period compared to the third (Table 3.9).

Blood urea N concentration differences in 1987 were due to TRT (P = 0.093) and to PER (P = 0.004) effects but not to their interaction (Table 3.6). Among PER, BUN concentration (mg 100 ml^{-1}) for NP (6.2) tended to be lower (P = 0.132) than the average for LO and HI (9.1) (Table 3.10). Blood urea N for HI (11.4) was higher (P = 0.057) than for LO (6.8). Mean BUN for 20 August (11.4 mg 100 ml^{-1}) was higher than for 30 July (5.5) and 10 September (8.6), and tended to be higher than for 1 October (9.4). In 1988, differences (P = 0.008) in BUN were due to PER only (Table 3.6), with mean BUN for 4 August (12.3) being higher than for 15 September (6.9) (Table 3.11). Blood urea nitrogen for LA (single replicate) appeared to be higher than the within period BUN means for steers on LG pasture treatments. Although not different within periods, BUN for HI in both years, and for LO in 1988 tended to be higher than for NP.

Forage Nutritive Value

A preliminary analysis for treatment (NP, LO, and HI) effects on LG pasture indicated that hand-plucked herbage CP and IVDOM concentration was not affected by supplementation. Therefore, hand-plucked herbage replicates for NP, LO, and HI treatments were treated as six replicates of LG pasture.

Table 3.10. Blood urea nitrogen (BUN) as affected by sampling date and pasture treatment in 1987.

Treatment[+]	Sampling date: 30 July	20 Aug.	10 Sept.	1 Oct.	Mean
	mg 100 ml^{-1}				
NP	3.6	10.4	3.0	8.0	6.2
LO	4.1	10.1	6.9	6.0	6.8
HI	10.0	13.3	11.4	10.9	11.9
LA	4.3	12.0	13.0	12.6	10.4
					(1.23)‡
Mean (0.85)#	5.5§	11.4	8.6¶	9.4	

Results of significance tests for planned comparisons among treatment means

Planned comparison	P value
NP vs. LO + HI	0.132
LO vs. HI	0.057
LA vs. LO + HI	0.423

[+] NP, LO, and HI are no, low, and high protein supplementation of limpograss pasture. LA is a limpograss-aeschynomene association.

‡ Standard error for treatment means over periods.

§,¶ Period mean over treatments differed from that on 20 August at $P \leq 0.001$ and $P \leq 0.01$, respectively.

Standard error for period means over treatments.

Table 3.11. Blood urea nitrogen (BUN) as affected by sampling date and pasture treatment in 1988.

Treatment[+]	Sampling date			
	4 Aug.	25 Aug	15 Sept.	6 Oct
	mg 100 ml^{-1}			
NP	9.8	5.7	4.2	3.6
LO	13.8	9.0	7.4	8.2
HI	13.4	10.2	9.0	11.2
Mean (0.89)[§]	12.3[‡]	8.3	6.9	7.7
LA[¶]	-	11.7	13.8	14.0

[+] NP, LO, and HI are no, low, and high protein supplementation of limpograss pasture. LA is a limpograss-aeschynomene association.
[‡] Period mean over treatments differed from that of 15 September at $P \leq 0.05$.
[§] Standard error for period means over treatments.
[¶] Data are for a single replicate and are presented for comparison purposes, only.

An interaction (P = 0.002) was observed in 1987 between sampling date and pasture type for hand-plucked herbage CP concentration (Table 3.12). The interaction effect on CP was primarily due to sampling date differences within LA. Hand-plucked LA herbage CP was higher for the second sampling date (84 g kg^{-1} DM) than for the first (67) and third (65) dates (Table 3.13), but similar to CP for the last date (84). Crude protein for LG herbage tended to be lower than for LA herbage within sampling dates. There was no difference in LG CP among sampling dates, with CP averaging 58 g kg^{-1} DM over the season. In 1988, there was a PER effect (P = 0.004) on CP concentration of LG pastures (Table 3.12). Crude protein concentration was highest for the first sampling date and tended to decline thereafter (Table 3.14). Crude protein for the first (83 g kg^{-1} DM) and second (87) sampling dates was higher than for the third (68). Crude protein for LG herbage on 28 September (72 g kg^{-1} DM) was similar to that for 7 September. Crude protein concentration for LA (single replicate) in 1988 (Table 3.14) appeared to be consistently higher over the grazing season relative to LA in 1987 (Table 3.13). Despite a general decline over the season, LG pasture CP also tended to be higher in 1988 than in 1987.

In 1987, there was a TYPE by DATE interaction (P = 0.004) for IVDOM (Table 3.12). For all dates but 25 August, hand-plucked LA IVDOM was higher than that of LG (Table 3.13). Within LG pastures, hand-plucked herbage IVDOM for 4

Table 3.12 Levels of probability for differences in hand-plucked herbage crude protein (CP) and in vitro digestible organic matter (IVDOM) concentration due to pasture type (TYPE), sampling date (DATE), and their interaction in 1987 and 1988.

	CP		IVDOM	
Effect	1987	1988[+]	1987	1988[+]
TYPE	0.002	-	0.003	-
DATE	0.016	0.004	0.003	0.397
DATE X TYPE	0.002	-	0.004	-

[+] Statistics are for one pasture type and only DATE is in the model.

Table 3.13. Least squares means for hand-plucked herbage crude protein (CP) and in vitro digestible organic matter concentration (IVDOM) in limpograss (LG) and limpograss-aeschynomene (LA) pastures during mid-summer to early fall in 1987.

Pasture type	Sampling Date[+] 15 July	4 Aug.	25 Aug	10 Sept
	---------- CP (g kg^{-1}) ----------			
LG	58a[‡]	58b	61a	58b
LA	87a[§]	94a	65a[§]	84a
SE[#]	4.2	3.9	4.8	7.8
	---------- IVDOM (g kg^{-1}) ----------			
LG	614b	611b	608a	584b[¶]
LA	682a	682a	620a[¶]	648a[¶]
SE[#]	12.9	10.6	9.0	13.3

[+] Dates are for LG pasture sampling, LA pastures were sampled the following week for each date.
[‡] Pasture means within dates followed by the same letter are not different ($P \leq 0.05$).
[§] Date mean within pasture types differed from that on 4 August ($P \leq 0.01$).
[¶] Date mean within pasture types differed from that on 4 August ($P \leq 0.05$).
[#] Largest standard errors for within sampling date means.

Table 3.14. Hand-plucked herbage crude protein (CP) and in vitro digestible organic matter (IVDOM) concentration in limpograss (LG) and limpograss-aeschynomene (LA) pastures during mid-summer to early fall in 1988.

Pasture type	Sampling Date[+] 28 July	17 Aug	7 Sept.	25 Sept
	---------- CP (g kg^{-1}) ----------			
LG	93[‡]	87[‡]	69	72
LA[§]	-	136	93	129
	--------- IVDOM (g kg^{-1}) ----------			
LG	577	567	570	565 NS
LA[§]	-	678	633	602

[+] Dates are for LG pasture sampling, LA pastures were sampled the following week for each date.
[‡] Date mean within LG differed from that on 4 August ($P \leq 0.01$).
[§] Means are for a single replicate and are presented for comparison, only.
NS $P > 0.05$.

August (611 g kg^{-1} OM) did not differ from herbage sampled on 15 July (614) and 25 August (606) but was higher than that from 16 September (584). Limpograss-aeschynomene pasture herbage IVDOM concentration for 4 August (682 g kg^{-1} OM) was higher than for 25 August (620) and for 16 September (648; Table 3.13). In 1988, there was no DATE effect (P = 0.397) on LG hand-plucked herbage IVDOM. Limpograss pasture herbage averaged 570 g kg^{-1} OM over the grazing season (Table 3.14).

Discussion

The primary objective in this experiment was to determine if limited protein supplementation (ie corn-urea) on LG pasture would improve animal performance during the time of the grazing season that is typically referred to as the summer slump period. Nonsupplemented steers grazing LG pasture averaged 0.29 kg d^{-1} gain over the two 84-d grazing seasons. This was slightly lower than the ADG (0.39 kg d^{-1}) reported by Rusland et al. (1988) for a 3-yr grazing study on LG pasture under similar management conditions. Supplementing steers on LG pasture with rations containing 123 g CP kg^{-1} (LO) and 500 g CP kg^{-1} (HI) daily resulted in approximately a 100% (0.28 kg d^{-1}) increase in daily gain over nonsupplemented steers. It has been suggested that supplementing with corn on pasture results in increased animal gains of 0.10 to 0.15 kg d^{-1} per kg of corn fed (W.E.

Kunkle, 1989, personal communication). Using these guidelines, supplementing with approximately 0.6 kg corn d^{-1} would account for less than 0.1 kg d^{-1} of the increase observed in ADG. Our data, therefore, suggest that higher daily gains with supplementation compared to no supplementation was primarily due to the urea component of the LO and HI supplements. Although mean seasonal ADG was higher for supplemented steers, within period differences could not be detected, probably due to high variation associated with measurements of short term weight changes (Matches, 1970).

Based on current prices, the cost of the LO and HI supplements (ingredients only) was approximately $ 0.10 and $ 0.13 $head^{-1}$ d^{-1}, respectively. For LO and HI supplements, this corresponds to costs of $ 0.42 and $ 0.43 per kg of gain above that observed on unsupplemented pastures. This suggests that supplementation has practical application for LG pastures in Florida.

Although herbage CP concentration tended to be higher in 1988 than in 1987, ADG was lower over treatments in 1988. Based on hand-plucked herbage data, the DOM to CP ratio for LG pastures in 1987 and 1988 were 10.4 and 7.1, respectively. Hogan and Weston (1981) have suggested that an N limitation to microbial protein synthesis appears likely when the ratio of DOM to CP in the diet exceeds 10. In 1987, when CP of LG did not exceed 62 g kg^{-1}, ADG on HI tended to be higher than

that on LO. The greater response in animal performance for HI compared to that for LO may have been due to the apparent lower DOM to CP ratio of the total diet of steers supplemented with the higher level of urea. The magnitude of the difference in BUN levels between HI and LO was also larger in 1987, and BUN concentration in steers on the LO treatment was below the recommended range of 8 to 10 mg 100 ml^{-1} described by Hammond (1987). When herbage CP concentrations were higher in 1988, the weight gain response to supplements LO and HI was the same, and BUN levels of steers on the LO treatment exceeded 9 mg 100 ml^{-1}. The DOM to CP ratio of LG pasture herbage in 1988 was well below 10 (e.g., 7.1). Hume et al. (1970) found no further increase in the flow of microbial protein out of the rumen when the DOM to CP ratio in purified cellulose-based diets fed to sheep was lowered from 7.4 to 4.2 by the addition of urea. Our data support the fact that the effectiveness of urea as a supplemental source of N is highly dependent on the total dietary DOM to CP ratio.

Daily gains for steers grazing LA were similar to those grazing LG with supplementation. Percentage asachynomene in pre-graze whole canopy herbage averaged only 8% in 1987 but appeared to make a significant contribution to the overall CP concentration of LA relative to the pure LG stands. In vitro organic matter digestibility for hand-plucked herbage was higher for LA than for LG pastures and can also be attributed

to the legume contribution to the LA sward. Deeplte the reletively low percentege of eeschynosene in LA peetures, animel daily gelne were 79% higher for LA than for non-eupplemented LG (NP). These results ere similar to the results of Ruslend et el. (1988) who reported 80% hlgher ADG on LA than on LG peeture.

Cerrying capeclty (kg llveweight ha^{-1} d^{-1}) wee greeter over the 2-yr study for LG then for LA peetures end reflected lower HA ee well es lower meen pre-greze herbege mese for LA than for LG peturee. Simller results were obtained by Ruelend et el. (1988). Supplementetion of low quellty forege with urea hee been reported to lnoresee OM intake (Kempton end Leng, 1979; Egen end Doyle, 1985). Despite obeerving lower CC for HI compared to LO, we were unable to detect hlgher herbage inteke for eteers on the HI treetment compared te LO treetment, ueing crude eward difference technlques.

Meen post-greze herbage mess wee lower for LA than LG peeturee hecauee LA peeturee were grezed to a lower etubble height. There were no differencee in post-greze herbage eees among the NP, LO, end HI treetments euggeetlng thet treetaent differencee in ADG were due to supplement end to pesture nutritive velue rether then quentlty of herbage.

Eerller etudiee have ehown increeeed digeetibility of forege wlth urea eupplementetlon (Coombe end Tribe, 1963; McAllen end Griffith, 1987; Bates et al., 1988). Although not determlned, increeeed in vlvo digeetibility of LG herbege

may have contributed to improved animal performance (ADG) with corn-urea supplementation compared to non-supplemented steers in the present study.

Gain per hectare on LG pasture over the 2 yr was higher for supplemented than non-supplemented steers. Low gains for LA were primarily related to low CC, particularly in 1988, rather than ADG. As discussed in the materials and methods section, severe drought in early summer prevented timely and successful establishment of aeschynomene in 1988. The occurrence of early season drought is not uncommon in Florida, and it reduces the reliability of warm-season annual legumes

Summary and Conclusions

A 2-yr grazing study was conducted to determine the effects of protein supplementation on animal performance of steers grazing LG pasture during the summer slump period. Average daily gain increased nearly 100% and gain per hectare increased 70% on LG pasture when steers received a corn-urea supplement. During the specific times in each grazing season when animal performance on the control was lowest, however, supplementation with corn-urea did not overcome the summer slump The greatest responses to supplementation occurred prior to and just after the specific period of lowest animal performance. Our data suggest that factors in addition to

inadequate dietary CP are likely contributing to the summer slump phenomenon but that supplementation with corn-urea is a potential alternative to overseeding legumes to improve animal gain during the mid-summer through early fall period of the grazing season. A more detailed description of the character and distribution of CP in the LG sward canopy may aid in determining to what extent CP availability functions to limit performance during the summer slump period.

The potential for improving ADG on LG pasture by including a legume such as aeschynomene has been confirmed in this study. However, its contribution to improving overall animal production is dependent upon favorable environmental conditions in late spring for timely and successful establishment. We conclude that supplementing steers grazing LG pasture with protein (as corn-urea) is a practical approach to improving animal performance during mid-summer through early fall in Florida and can reduce the adverse effects of the summer slump on seasonal animal production.

CHAPTER IV

CHARACTERIZATION OF CANOPY STRUCTURE AND HERBAGE NUTRITIVE VALUE IN LIMPOGRASS PASTURES DURING MID-SUMMER TO EARLY FALL

Introduction

The term "summer slump" has been used to describe a period of time when a decline is observed in average daily gain (ADG) of cattle (Bos spp.) grazing summer pasture. In Florida, a summer slump in ADG is usually observed between late July through September on tropical grass pastures such as limpograss [Hemarthria altissima (Poir.) Stapf et C.E. Hubb.] (Rueland et al., 1988).

A distinction needs to be made between the summer slump phenomenon and the general seasonal depression in animal performance observed on unimproved tropical and subtropical grass pastures during the dry or cool seasons (Lee et al., 1987; Stephenson et al., 1983; Van Niekirk and Jacobs, 1985). In these cases, poor animal performance has been attributed to low crude protein (CP) concentration and/or dry matter (DM) digestibility and slow growth rate of grasses during this time of the year (Milford, 1960; Wilson and Minson, 1980). During the summer slump in Florida, growth rates of limpograss (LG) are high and forage matures rapidly. There

may not, however, be a correlation between CP or in vitro digestible organic matter (IVDOM) concentration and ADG (Rusland et al., 1988).

There has been much speculation as to the cause of the depression in animal performance under grazing conditions In a recent study, ADG of steers grazing 'Mott' dwarf elephantgrass (Pennisetum purpureum Schum.) pastures at the same location as animals grazing LG pastures showed no decline in gain during summer (Sollenberger et al., 1988b). Based on the contrasting results between grasses, it was suggested that the summer slump on LG pasture was related to environmental effects on LG herbage rather than direct effects on the animal itself (Rusland et al., 1988).

A dominant feature of plant-animal interactions is diet selection when cattle consume pasture herbage (Raymond, 1968). The potential for selectivity is initially dependent on the canopy structure of the sward that is presented to the animal (Mennstjs and Eberenhn, 1980). Canopy height (Taylor and Rudmen, 1966; Stobbs, 1973a) the proportions of leaf and stem material within the canopy (Stobbs, 1973b; Wilson and Mineon, 1980), and their bulk density (Stobbs, 1973c) all contribute to the degree of selectivity, the intrinsic availability of herbage to the animal (Allden and Whittaker, 1970), and the ultimate prehension of plant material.

Variation in N concentration and digestibility of plant material by plant part and maturity has been well documented

in the literature. Nitrogen concentration (hence, CP concentration) of leaf material is generally higher than that of stems and petioles, and younger plant material often has higher N concentration than more mature herbage (Mineon, 1971). Due to the relatively high percentage of stem in many tropical grasses (Wilson and Minson, 1980; Sollenberger et al., 1988a), greater morphological and compositional variability can occur vertically through the sward canopy of tropical grasses ('t Mannetje and Ebersohn, 1980; Stobbs, 1973b) than with temperate species. Therefore, selectivity of herbage under grazing conditions greatly affects the actual prehension of plant CP and DOM.

Detailed canopy characterization data from rotationally-grazed LG pastures are lacking and may aid in determining what plant factors are associated with low summer ADG. This study was conducted to identify and describe changes in 'Floraite' LG canopy structure and forage nutritive value during mid-summer to early fall and to make inferences about the effect of forage factors on steer daily gains during this time of the season.

Materials and Methods

The experiment was conducted in 1987 and 1988 at the Forage Evaluation Field Laboratory of the Beef Research Unit near Gainesville, Florida. Limpograss pastures used in this

study were part of the animal grazing study and have been described in Chapter III.

Starting on 15 July 1987, LG pastures were sampled every 21 d through 16 September. These sampling dates were chosen to coincide with a concurrent 84-d grazing study that commenced on 9 July such that each of the four sampling dates fell within one of the four 21-d grazing periods. Samples were taken pre-graze, alternately on paddocks 1 and 4 in each pasture, during the grazing season. Paddocks 2 and 3 were sampled in a similar manner in 1988 starting 28 July through 28 September. In 1988 the concurrent 84-d grazing study was initiated on 14 July. Due to the rotational grazing management of the pastures, pre-graze samples on paddocks 1 and 4 (1987) and 2 and 3 (1988) consisted of 5-wk regrowth and were considered to be representative of available herbage on each of the 3 paddocks grazed between sampling dates.

Four pre-graze sample sites (0.5 m^2) were selected in the respective paddocks to represent mean forage availability and pasture condition. Within each pre-graze sample site, the grazed horizon (determined as the difference between total canopy height and a 5-cm base stubble) was divided into two layers of equal height. A sampling platform (1.0 m X 0.5 m) that was vertically adjustable in 5-cm increments was used as a guide for delineating and clipping the respective layers within a sample site. The purpose of dividing the canopy

into two layers was to allow for a more descriptive characterization of the sward canopy.

Herbage from the upper layer (UL) was clipped, bagged, and cold-stored (4.5°C) until subsequent separation. Herbage from the lower layer (LL) was clipped at the 5-cm base stubble height and collected in an identical manner as UL. All pasture samples were subsequently hand-separated into LG, weed (WEED), and dead (DEAD) components. Limpograss within the upper and lower layers was further separated into leaf blade (LEAF; ULL and LLL, respectively) and stem plus sheath (STEM; ULS and LLS, respectively) fractions; inflorescences, when present were included with the stem fraction. All botanical components and LG fractions were forced-air dried at 60°C for 48 h. Dried components and LG fractions were weighed and DEAD material discarded. Each LG fraction and the WEED component from a given data were composited over sample sites within layers and within pastures.

Composite samples were ground to pass a 1-mm screen, and used for subsequent N and IVDOM analysis. A modified aluminum block digestion procedure (Gallaher et al., 1975) and semi-automated colorimetry (Hambleton, 1977) were used for all N determinations. Crude protein was calculated as N X 6.25 on a DM basis. In vitro digestible organic matter concentration was determined using a modified two-stage digestion procedure (Moore and Mott, 1974).

Total green herbage CP and IVDOM concentration are reported for layers and whole canopy (combined layers) and were determined by calculating the sum of weighted contributions of WEED and LG LEAF and STEM within a layer for each variable. Crude protein and IVDOM concentration are also reported for LG by fraction, layer, and whole canopy. Limpograss leaf/stem ratio (LSR) within layers and for whole canopy is on a DM basis. Canopy height for whole canopy is based on total canopy height minus a 5-cm base stubble. Total herbage DM bulk density (DMBD) is calculated as the product of g total DM m^{-2} and layer height, and is reported on a g m^{-3} basis. Whole canopy DMBD is based on combined layer data. Limpograss herbage mass (HM, g DM m^{-2}) is reported by fraction, layer, and whole canopy. Total green herbage CP bulk density (CPBD) for each layer is calculated as the sum of LG fractions (leaf and stem) and WEED g CP m^{-2} multiplied by layer height and is reported in total g CP m^{-3}.

The experimental design was completely randomized. Supplement treatment (see Chapter III) had no effect on canopy structure or nutritive value, so there were 6 and 4 replications of LG pastures in 1987 and 1988, respectively. Only four replicates were used in 1988 because canopies of the low supplement treatment were not stratified or separated into leaf and stem. Statistics for botanical composition were conducted following arcsine transformation of the data. Botanical composition means presented in the results have

bean transformed back to original scale (i.e., percentage) and, therefore, standard errors are not reported.

Statistical analyses were performed separately for LG fraction, canopy layer, and whole canopy data. Repeated measures (sampling date) analysis of variance procedures were used. Statistics are based on the univariate approach with degrees of freedom correction. Mean comparisons of LG fractions within sampling dates were by Duncan's multiple range test (DMRT). Comparisons of fraction means over sampling dates when appropriate ($P \leq 0.05$) were made using single degree of freedom contrasts, due to restrictions imposed by repeated measures analysis. Between sampling date comparisons (when appropriate) were done with preplanned contrasts. Selection of sampling date contrasts was based on comparing the sampling date that corresponded to the grazing period of lowest animal performance (from Chapter III) for each year with each of the other three dates. Therefore, the second sampling date in 1987 and the third sampling date in 1988 were each compared to the other three dates within that year.

Results

Botanical composition and dry matter distribution: 1987

There was no sampling date by layer interaction for any of the botanical components (Table 4.1). Percentage weed did not differ between layers ($P = 0.701$) or among sampling dates ($P = 0.387$) and averaged 6% over the entire season (data not shown). Percentage LG (GRASS) and DEAD varied invarsely. Percentage DEAD material was greater in LL (17%) than UL (6%) and, as a percentage of whole canopy herbage mass, increased ($P < 0.001$; Table 4.2) over time (Table 4.3). Limpograss was a higher percentage of UL (89 %) herbage mass than LL (76%) and tended to decrease over time.

There was no interaction between layer and sampling date ($P < 0.576$) for LG LSR (Table 4.4), nor were there differences in LSR due to date ($P = 0.258$; Table 4.4). Mean UL LSR (0.38) was greater than LL (0.10) for the entire season (Table 4.5). Whole canopy LSR did not change over the season ($P = 0.112$, Table 4.6) and averaged 0.18 (Table 4.5).

There was an interaction between fraction and sampling date ($P = 0.024$, Table 4.7) for LG HM. The distribution of HM (g DM m^{-2}) among canopy fractions showed greater differences due to fraction than to sampling date (Table 4.8). Upper layer leaf HM tended to be greater than LLL which constituted the smallest proportion of whole canopy HM.

Table 4.1. Levels of probability for differences in percentage dead (DEAD), limpograss (GRASS), and weed (WEED) in total herbage due to layer (L), sampling date (D), and their interaction in limpograss pastures in 1987 and 1988.

Effect	Response Variable		
	DEAD	GRASS	WEED
		1987	
L	***	0.005	0.701
D	***	***	0.387
D X L	0.166	0.300	0.726
		1988	
L	***	0.002	0.312
D	***	0.020	0.407
D X L	***	0.006	0.702

*** $P < 0.001$.

Table 4.2. Levels of probability for differences in whole canopy percentage dead (DEAD), limpograss (GRASS), and weed (WEED) in total herbage due to sampling date (D) in limpograss pastures in 1987 and 1988.

	Response Variable		
Effect	DEAD	GRASS	WEED
		1987	
D	***	***	0.496
		1988	
D	***	0.127	0.629

*** $P < 0.001$.

Table 4.3. Canopy layer and whole canopy botanical composition of 5-wk limpograss pasture regrowth during mid-summer to early fall in 1987.

Canopy component	Sampling Date				Mean
	15 July	4 Aug.	25 Aug.	18 Sept.	
	%				
	Dead Material				
Layer					
UL	0	2	5	15	8[+]
LL	7	12	22	28	17
Mean	4[‡]	7	14[‡]	22[‡]	
Whole canopy					
	5[§]	10	17[§]	24[§]	
	Limpograss				
Layer					
UL	94	94	88	81	89[+]
LL	86	81	71	88	78
Mean	90[‡]	88	80[‡]	74[‡]	
Whole canopy					
	88	84	76[§]	70[§]	

[+] Layer means over dates differed ($P \leq 0.05$).
[‡] Period mean over layers differed from that on 4 August ($P \leq 0.05$).
[§] Whole canopy percentage dead or limpograss differed from that on 4 August ($P \leq 0.05$).

Table 4.4. Levels of probability for differences in limpograss leaf/stem ratio (LSR), total herbage dry matter bulk density (DMBD), total green herbage crude protein concentration (CP) and CP bulk density (CPBD), and total green herbage in vitro digestible organic matter (IVDOM) due to canopy layer (L), sampling date (D), and their interaction in 1987 and 1988

	Response Variables				
Effect	LSR	DMBD	CP	CPBD	IVDOM
			1987		
L	***	***	***	0.002	***
D	0.258	0.001	0.010	0.001	***
D X L	0.576	0.004	0.018	0.001	0.974
			1988		
L	***	***	***	***	0.017
D	***	0.003	***	0.001	0.464
D X L	0.002	0.007	0.018	0.013	0.206

*** $P < 0.001$.

Table 4.5. Canopy layer and whole canopy limpograss leaf/stem ratio of 5-wk limpograss pasture regrowth during mid-summer to early fall in 1987.

Canopy component	Sampling Date				
	15 July	4 Aug.	25 Aug.	16 Sept.	Mean
Layer					
UL	0.42	0.35	0.39	0.36	0.38[+]
LL	0.11	0.09	0.09	0.10	0.10
					(0.022)[‡]
Whole canopy					
	0.22	0.15	0.17	0.18	NS
(0.026)[§]					

[+] Layer means over dates differed ($P \leq 0.05$).
‡,§ Standard errors for layer means over dates and whole canopy means, respectively.
NS $P > 0.05$.

Table 4.6 Levels of probability for differences in canopy height (HT), and whole canopy limpograss leaf/stem ratio (LSR), total herbage dry matter bulk density (DMBD), total green herbage crude protein concentration (CP) and CP bulk density (CPBD), and total green herbage in vitro digestible organic matter (IVDOM) concentration due to sampling date (D) in 1987 and 1988.

	Response Variables					
Effect	HT	LSR	DMBD	CP	CPBD	IVDOM
			1987			
D	***	0.112	0.006	0.018	0.003	0.001
			1988			
D	***	***	0.005	***	0.003	0.112

*** $P < 0.001$.

Table 4.7. Levels of probability for differences in limpograss herbage crude protein (CP) and in vitro digestible organic matter (IVDOM) concentration, and limpograss herbage mass due to canopy fraction (F), canopy layer (L), sampling date (D), and their interactions, and whole canopy analysis by sampling date in 1987.

	Response Variables		
Effect	CP	IVDOM	HM
Canopy Fraction Analysis:			
F	***	***	***
D	0.109	***	0.148
D X F	0.003	0.207	0.024
Canopy Layer Analysis:			
L	***	***	0.001
D	0.033	***	0.173
D X L	0.036	0.935	0.031
Whole Canopy Analysis:			
D	0.015	0.045	-

*** $P < 0.001$.

Table 4 8. Limpograss herbage mass for canopy fraction and layer 5-wk limpograss pasture regrowth in 1987.

Canopy component	Sampling Date: 15 July	4 Aug.	25 Aug.	18 Sept.
	g DM m^{-2}			
Fraction				
ULL	92c[+]	58b	66c	57c
ULS	222b	186b	189b	165b
LLL	48c	47b	37c	42c
LLS	415a[‡]	580a	428a[‡]	418a[‡]
SE	41.1	81.4	45.0	34.7
Layer				
Upper	314[§]	224	234[§]	222
Lower	462[¶]	607	488[¶]	480
SE	68.1	91.2	88.2	50.1

[+] Fraction means within dates followed by the same letter are not different at the 0.05 level by DMRT.
[‡] Date mean within fractions differed from that on 4 August ($P \leq 0.05$).
[§] The magnitude of the difference between layers within a sampling date differed from that on 4 August ($P \leq 0.05$).
[¶] Date mean within layers differed from that on 4 August ($P \leq 0.05$).
SE Standard error of the mean.

The greatest proportion of whole canopy DM was in LLS within each sampling date. Lower layer stem DM was greatest on 4 August and was the major contributor to differences in layer DM over the season. There was an interaction between layer and sampling date for DM ($P = 0.031$, Table 4.7). Layer differences in DM within both the first and third sampling dates were not as great as the difference between layers for the second sampling date. Layer DM differences for the last sampling date were similar to those for the second date.

There was an interaction ($P = 0.004$) between layer and sampling date for total herbage DMBD (Table 4.4). Planned contrasts of sampling dates within each layer (i.e., the second sampling date versus each of the other sampling dates) revealed that the interaction was due to the magnitude of the layer difference for the first sampling date being less than for the second date (Table 4.9). Lower layer DMBD tended to increase over time compared to no change in UL DMBD. Upper canopy layer DMBD ranged from 868 g m^{-3} on 4 August to 1335 g m^{-3} on 16 September. Analysis of whole canopy DMBD (Table 4.6) showed similar trends as LL data. When compared to 4 August (1791), only 15 July (1519) was lower in whole canopy DMBD (Table 4.9). There was a trend toward an increase in whole canopy DMBD over time, as is reflected in sampling date means for LL DMBD.

Canopy height was highest for the first two sampling dates (58 and 55 cm, respectively) (Table 4.9). Canopy

Table 4.9. Total herbage dry matter bulk density (DMBD) for canopy layer and whole canopy, and canopy height of 5-wk ilepograss pasture regrowth during mid-summer to early fall in 1987

Canopy component	Sampling Date			
	15 July	4 Aug.	25 Aug.	16 Sept.
	DMBD			
	g DM m^{-3}			
Layer				
UL	1171+	868	1182	1335
LL	1868‡	2714	2866	3300
SE§	247.1	368.9	379.8	205.4
Whole canopy				
(191.4)#	1519¶	1791	2024	2317
	Canopy Height			
	cm			
Whole canopy				
(2.4)#	58	55	46++	42++

+ The magnitude of the difference between layers within a sampling date differed from that on 4 August ($P \leq 0.05$).
‡ Data mean within layers differed from that on 4 August ($P \leq 0.05$).
§ Standard error of the mean.
¶ Mean differed from that on 4 August ($P \leq 0.05$).
# Standard error for whole canopy sampling date means.
++ Mean differed from that on 4 August $P \leq 0.05$).

height for 25 August (46 cm) and 15 September (42) were both lower than for 4 August.

In vitro digestible organic matter concentration: 1987

There was no layer by sampling date interaction (P = 0.974, Table 4.4) for total green herbage IVDOM concentration. Upper layer IVDOM averaged 585 g kg^{-1} OM over the season and was greater than LL (519 g kg^{-1} OM; Table 4.10). There was a general decline in IVDOM over the season, however, only whole canopy IVDOM for 16 September was different from that for 4 August.

There was no interaction between canopy fraction and sampling date (P = 0.207) for LG herbage IVDOM concentration (Table 4.7). Mean IVDOM for ULL was not different from LLL (Table 4.11). Upper layer stem IVDOM was greater than LLL and LLS IVDOM and tended to be greater than ULL IVDOM. Within each fraction, IVDOM concentration decreased over time, however, the effect of sampling date appeared to be greater on stem fractions than leaf fractions. When analyzed by layer, IVDOM was greater for UL than LL for all sampling dates. Whole canopy IVDOM tended to decrease over time but single degree of freedom contrasts revealed no differences between 4 August and each of the other sampling dates.

Table 4.10. Total green herbage in vitro digestible organic matter concentration for canopy layer and whole canopy 5-wk limpograss pasture regrowth during mid-summer to early fall in 1987.

Canopy component	Sampling Date				Mean
	15 July	4 Aug.	25 Aug.	16 Sept.	
	g kg^{-1}				
Layer					
UL	602	594	579	564	585[+]
LL	539	530	510	497	519
Mean	570	582	544	530[#]	(5.5)[‡]
(6.8)[§]					
Whole canopy					
(8.8)[¶]	584	547	534	518[++]	

[+] Layer means over dates differed ($P \leq 0.05$).
[‡],[§],[¶] Standard errors for layer means over dates, date means over layers, and whole canopy means, respectively.
[#] Date mean over layers differed from that on 4 August ($P \leq 0.05$).
[++] Mean differed from that on 4 August ($P \leq 0.05$).

Table 4.11. Limpograss herbage in vitro digestible organic matter concentration for canopy fraction, layer, and whole canopy 5-wk limpograss pasture regrowth in 1987

Canopy component	Sampling Data: 15 July	4 Aug.	25 Aug.	16 Sept.	Mean	Contrast[+]: ULL	ULS
	---------- g kg^{-1} ----------						
Fraction							
ULL	564	566	552	544	556		
ULS	628	610	588	578	604		
LLL	544	568	535	528	544	NS	**
LLS	550	534	516	503	526		***
Mean (5.6)[§]	572	570	550[¶]	538[¶]	(7.8)[‡]		
Layer							
Upper	609	588	585	570	590[#]		
Lower	550	537	518	506	528		
Mean (6.4)[‡‡]	580	568	552	538[§§]	(7.8)[++]		
Whole canopy							
(17.8)[¶¶]	573	554	541	504			

,*,NS P ≤ 0.01 and 0.001, and P > 0.05, respectively.

+ Preplanned single df contrasts to test differences in fraction means over dates.

‡,§ Standard errors for fraction means over dates and date means over fraction, respectively.

¶ Date mean over fractions differed from that on 4 August (P ≤ 0.05).

Layer means over dates differed (P ≤ 0.05).

++,‡‡ Standard errors for layer means over dates and date means over layers, respectively.

§§ Date mean over layers differed from that on 4 August (P ≤ 0.05).

¶¶ Standard error for whole canopy date means. Preplanned contrasts did not describe the date effect.

Crude protein concentration and distribution: 1987

There was a sampling date by layer interaction ($P = 0.018$) for total green herbage CP concentration in 1987 (Table 4.4). Within layers, UL CP concentration differed among sampling dates but LL CP did not vary over the season (Table 4.12). Upper layer CP was always higher than LL but the magnitude of difference varied among sampling dates. Whole canopy CP for 4 August (40 g kg^{-1}) was lower than for 15 July (47; $P < 0.05$) and 25 August (47; $P < 0.10$) but was not different from that for 16 September (44).

There was a fraction by sampling date interaction for LG herbage CP concentration ($P = 0.003$, Table 4.7). For the first two sampling dates, ULL had the highest CP concentration, but ULL and LLL did not differ in CP for the last two sampling dates (Table 4.13). Crude protein concentration for LLS was consistently lower than for any other fraction regardless of sampling date and averaged 30 g kg^{-1} over the season. In general, leaf CP concentration (regardless of layer) was two to three times greater than stem. Layer CP concentration, weighted for fractions, was greater for UL than LL for all but the last sampling date. Lower layer CP concentration remained relatively constant over the season whereas UL CP varied. On a whole canopy basis, LG herbage CP concentration was greatest for the first

Table 4.12. Total green herbage crude protein concentration for canopy layer and whole canopy 5-wk limpograss pasture regrowth during mid-summer to early fall in 1987.

Canopy component	Sampling Date			
	15 July	4 Aug.	25 Aug.	16 Sept.
	g kg^{-1}			
Layer				
UL	63†‡	54	61‡	52
LL	37	36	39	39
SE§	2.2	2.4	3.4	4.4
Whole canopy				
(2.1)#	47¶	40	47	44

† The magnitude of the difference between layers within a sampling date differed from that on 4 August ($P \leq 0.05$).
‡ Date mean within layer differed from that on 4 August ($P \leq 0.05$).
§ Standard error of the mean.
¶ Mean differed from that on 4 August ($P \leq 0.05$).
# Standard error for whole canopy sampling date means.

Table 4.13. Limpograss herbage crude protein concentration for canopy fraction, layer, and whole canopy 5-wk limpograss pasture regrowth in 1987.

Canopy component	Sampling Date: 15 July	4 Aug	25 Aug.	16 Sept.
	g kg^{-1}			
Fraction				
ULL	89a[+]	95a	100a	98a
ULS	49c	36c	41b	38b
LLL	72b	88b	91a	94a
LLS	31d[‡]	28d	30c	30c
SE	8.1	2.8	4.5	3.6
Layer				
Upper	61x[§¶]	52x	57x	48y
Lower	35y	33y	35y	36y
SE	3.0	2.0	4.8	5.9
Whole canopy				
(2.0)[++]	45[#]	38	43	40

[+] Fraction means within dates followed by the same latter are not different at the 0.05 level by DMRT.
[‡] Date mean within fraction differed from that on 4 August ($P \leq 0.05$).
[§] Layer means within dates followed by the same latter are not different ($P \leq 0.05$).
[¶] Date mean within layer differed from that on 4 August ($P \leq 0.05$)
[#] Mean differed from that on 4 August ($P \leq 0.05$).
[++] Standard error for whole canopy date means.
SE Standard error of the mean.

sampling date (45.5 g kg^{-1}) and tended to be lowest for 4 August.

There was an interaction (P = 0.001) between layer and sampling date for total green herbage CPBD in 1987 (Table 4.4). This was due to CPBD being similar between layers on 15 July but higher in the LL on all other dates (Table 4.14). There was no difference in the ratio of UL to LL CPBD between 4 August (0.49) and 25 August (0.65) or 18 September (0.54) but the ratio of UL to LL CPBD for 15 July (1.04) was greater than for 4 August. Lower layer CPBD tended to increased over time while UL CPBD remained relatively constant except for 4 August when UL CPBD was only 47 g m^{-3}.

When analyzed on a whole canopy basis (Table 4.6), there was a sampling date effect (P = 0.003) on total green herbage CPBD such that CPBD was higher for 25 August (93 g m^{-3}) and 16 September (101) than for 4 August (72). Whole canopy CPBD for 15 July (72 g m^{-3}) was not different from 4 August (Table 4.14).

Botanical composition and dry matter distribution: 1988

As in 1987, there was no layer (P = 0.312) or date (P = 0.407) effect on WEED percentage (Teble 4.1) nor was there a sampling date effect on whole canopy WEED percentage (P = 0.829, Table 4-2). The WEED component for whole canopy averaged 8% of total herbage over the 1988 season (data not

Table 4.14. Total green herbage crude protein bulk density for canopy layer and whole canopy 5-wk limpograss pasture regrowth during mid-summer to early fall 1987.

Canopy component	Sampling Date			
	15 July	4 Aug.	25 Aug.	16 Sept.
	---------- g m^{-3} ----------			
Layer				
UL	73[+‡]	47	72‡	70
LL	70‡	96	110	129‡
SE[§]	13.0	12.3	12.7	12.7
Whole canopy				
(7.6)[#]	72	72	93[¶]	101[¶]

[+] The magnitude of the difference between layers within a sampling date differed from that on 4 August ($P \leq 0.05$).
‡ Date mean within layer differed from that on 4 August ($P \leq 0.05$).
§ Standard error of the mean.
¶ Mean differed from that on 4 August ($P \leq 0.05$).
[#] Standard error for whole canopy sampling date means.

shown). There was a sampling date by layer interaction ($F < 0.001$) for percentage DEAD (Table 4.1). Dead herbage accounted for 20% of total LL herbage mass and 12% of whole canopy herbage for the first sampling date (28 July; Table 4.15). Following the first sampling date, dead material decreased sharply as a percentage of whole canopy herbage for 17 August (2%) but then tended to increase for the remainder of the season.

There was a layer by sampling date interaction ($P = 0.006$, Table 4.1) for percentage LG that was due to between layer differences being greater for the first sampling date than for other dates (Table 4.15). Limpograss accounted for 94% of UL herbage and 74% of LL herbage for 28 July. Limpograss as a percentage of whole canopy herbage mass did not differ between sampling dates and averaged 84% over the season.

Analysis of LG LSR in 1988 (Table 4.4) showed a sampling date by layer interaction ($P = 0.002$). The LSR for UL and LL on 28 July was 1.11 and 0.22, respectively, and their difference was greater than for 7 September when UL and LL LSR was 0.60 and 0.10, respectively (Table 4.16). Leaf/stem ratio by layer for 17 August and 28 September were not different from that for 7 September. A sampling date effect (Table 4.16) for whole canopy LSR was due to the high LSR for the first sampling date as was described above.

Table 4.15. Canopy layer and whole canopy botanical composition of 5-wk limpograss pasture regrowth during mid-summer to early fall in 1988.

Canopy component	Sampling Date			
	28 July	17 Aug.	7 Sept.	28 Sept.
	---------- % ----------			
	Dead Material			
Layer				
UL	1	0	0	5+
LL	20+	5+	9	12
Whole canopy				
	12‡	2‡	6	11‡
	Limpograss			
Layer				
UL	94§	94	92	89
LL	74+	89	85	84
Whole canopy				
	82	89	84	81 NS

+ Date mean within layers differed from that on 7 September ($P \leq 0.05$).
‡ Mean differed from that on 7 September ($P \leq 0.05$).
§ The magnitude of the difference between layers within a sampling data differed from that on 7 September ($P \leq 0.05$).
NS $P > 0.05$.

Table 4.16. Canopy layer and whole canopy limpograss leaf/stem ratio of 5-wk limpograss pasture regrowth during mid-summer to early fall in 1988.

Canopy component	Sampling Date			
	28 July	17 Aug.	7 Sept.	28 Sept.
Layer				
UL	1.11[+‡]	0.62	0.60	0.69
LL	0.22[‡]	0.15	0.10	0.14
SE[§]	0.054	0.022	0.054	0.057
Whole canopy				
(0.021)[#]	0.42[¶]	0.26	0.20	0.23

[+] The magnitude of the difference between layers within a sampling date differed from that on 7 September ($P \leq 0.05$).
[‡] Date mean within layers differed from that on 7 September ($P \leq 0.05$).
[§] Standard error of the mean.
[¶] Mean differed from that on 7 September ($P \leq 0.05$).
[#] Standard error for whole canopy sampling date means.

There was an interaction ($P < 0.001$) between fraction and sampling date (Table 4.17) for LG HM. As in 1987, the distribution of HM (g DM m^{-2}) among canopy fractions showed greater differences due to fraction than to sampling date (Table 4.16). Stem HM in both UL and LL as well as ULL HM tended to be greater during the middle of the season than at either the beginning or end. Leaf HM in LL did not change over time and averaged 53 g m^{-2}. Lower layer stem HM contributed the most to whole canopy HM at all sampling dates. A greater proportion of HM was observed in the LL compared to UL and this relationship did not change over time. The greatest difference in HM between layers was observed on 7 September when UL and LL HM were 187 and 568 g m^{-2}, respectively.

Effects of layer and sampling date on total herbage DMSD in 1988 (Table 4.4) were similar to those in 1987 (Tables 4.7 and 4.19). Upper layer DMSD remained constant over the season and averaged 846 g m^{-3} (Table 4.19). With the exception of 28 July, there was a tendency for LL DMSD to increase as the season progressed. Sampling date effects on whole canopy DMSD (Table 4.6) were similar to sampling date effects on LL DMSD, indicating changes in LL DMSD contributed greatly to changes in whole canopy DMSD.

Canopy height changed over time ($P = 0.005$, Table 4.6). Canopy height was lower for the first (34 cm) and last (36) sampling dates than for 7 September (52). Canopy height was

Table 4.17. Levels of probability for differences in limpograss herbage crude protein (CP) and in vitro digestible organic matter (IVDOM) concentration and limpograss herbage mass due to canopy fraction (F), canopy layer (L), sampling date (D), and their interactions, and whole canopy analysis by sampling date in 1986.

	Response Variables		
Effect	CP	IVDOM	HM
Canopy Fraction Analysis:			
F	***	0.001	***
D	***	0.181	***
D X F	0.025	0.004	***
Canopy Layer Analysis:			
L	***	0.012	***
D	***	0.349	***
D X L	0.007	0.158	0.005
Whole Canopy Analysis:			
D	0.002	0.107	-

*** P < 0.001.

Table 4.18. Limpograss herbage mass for canopy fraction and layer 5-wk limpograss pasture regrowth in 1988.

Canopy component	Sampling Date: 28 July	17 Aug.	7 Sept.	28 Sept
	g DM m^{-2}			
Fraction				
ULL	69b[+]	84bc	71c	55c
ULS	63b[‡]	138b	126b	81b[‡]
LLL	51b	57c	53c	52c
LLS	227a[‡]	411a[‡]	514a	390a[‡]
SE	16.0	34.6	16.9	14.0
Layer				
Upper	131[§]	221	197	136
Lower	278[¶]	469	568	442[¶]
SE	28.7	50.7	24.9	17.5

[+] Fraction means within dates followed by the same lattar are not different at the 0.05 level by DMRT.
[‡] Data mean within fractions differed from that on 7 September ($P \leq 0.05$).
[§] The magnitude of the difference between layers within a sampling date differed from that on 7 September ($P \leq 0.05$).
[¶] Data mean within layers differed from that on 7 September ($P \leq 0.05$).
SE Standard error of the mean.

Table 4.19. Total herbage dry matter bulk density (DMBD) for canopy layer and whole canopy, and canopy height of 5-wk limpograss pasture regrowth during mid-summer to early fall in 1988.

Canopy component	Sampling Date			
	28 July	17 Aug.	7 Sept.	28 Sept.
	DMBD g m^{-3}			
Layer				
UL	880	792[+]	826	887
LL	2333	1746[‡]	2588	3066
SE[§]	163	100	183	192
Whole canopy				
(96)[§]	1431	1203[¶]	1578	1784
	Canopy height			
	cm			
Whole canopy				
(2.2)[§]	34[++]	59[++]	52	36[++]

[+] The magnitude of the difference between layers within a sampling date differed from that on 7 September ($P \leq 0.05$).
[‡] Date mean within layers differed from that on 7 September ($P \leq 0.05$).
[§] Standard error of the mean.
[¶] Mean differed from that on 7 September ($P \leq 0.05$).
[§] Standard error for whole canopy sampling date means.
[++] Mean differed from that on 7 September $P \leq 0.05$).

highest for 17 August (59) and was higher than for 7 September (Table 4.19).

In vitro digestible organic matter concentration: 1988

Differences in total green herbage IVDOM concentration in 1988 occurred only due to layer ($P = 0.017$, Table 4.4). Mean UL IVDOM (562 g kg^{-1} OM) was higher than for LL (530) (Table 4.20). Whole canopy IVDOM did not differ due to sampling date ($P = 0.112$, Table 4.6) but did tend to decline over the season.

There was an interaction between fraction and sampling date ($P = 0.004$) for LG herbage IVDOM concentration in 1988 (Table 4.17). Within each of the first three sampling dates, ULS IVDOM was greater than that of ULL, LLL, and LLS (Table 4.21). For the last sampling date (28 September) there was no difference in IVDOM between ULL (558 g kg^{-1}), ULS (568), and LLL (561) but each was greater than for LLS (514). Within each fraction, there were no clear trends for sampling date effects on IVDOM concentration. Layer differences in IVDOM concentration were similar to those in 1987 in that UL (564) was greater than LL (532). Whole canopy LG IVDOM did not differ between sampling dates and averaged 541 g kg^{-1} over the season.

Table 4 20. Total green herbage in vitro digestible organic matter concentration for canopy layer and whole canopy 5-wk limpograss pasture regrowth during mid-summer to early fall in 1988.

Canopy component	Sampling Date				
	28 July	17 Aug.	7 Sept.	28 Sept.	Mean
	---------- g kg^{-1} ----------				
Layer					
UL	575	552	558	561	562†
LL	530	536	534	519	530
					(9.6)‡
Whole canopy					
	548	841	540	529 NS	

† Layer means over dates differed ($P \leq 0.05$).
‡ Standard error for layer means over dates.
NS $P > 0.05$.

Table 4.21. Limpograss herbage in vitro digestible organic matter concentration for canopy fraction, layer, and whole canopy 5-wk limpograss pasture regrowth in 1988.

Canopy component	Sampling Date				
	28 July	17 Aug.	7 Sept.	28 Sept.	
	g kg^{-1}				
Fraction					
ULL	554b[+]	504b	538b	558a	
ULS	601a	582a	583a	588a	
LLL	519b	518b	538b	561a	
LLS	534b	542b	539b	514b	
SE	18	18	18	14	
Layer					Mean
Upper	576	552	586	564	564[‡]
Lower	531	539	540	519	532
					(5.5)[§]
Whole canopy					
	546	543	546	530 NS	

[+] Fraction means within dates followed by the same letter are not different at the 0.05 level by DMRT.
[‡] Layer means over dates differed ($P \leq 0.05$).
[§] Standard error of layer means over dates.
SE Standard error of the mean.
NS $P > 0.05$.

Crude protein concentration and distribution: 1988

There was a sampling date by layer interaction for total green herbage CP concentration (P = 0.018, Table 4.4). This was due to the difference between UL (104 g kg^{-1}) and LL (54) CP concentration for 28 July being greater than that between UL (72) and LL (38) for 7 September (Table 4.22) Upper layer and LL CP concentration for 17 August (85 and 47 g kg^{-1} respectively) and 28 September (68 and 43) were not different from respective layers for 7 September. Whole canopy CP concentration for total green herbage was lower (Table 4.6) for 7 September then for each of the other three sampling dates (Table 4.22).

Compared to 1987, LG CP concentration in 1988 generally was greater for all fractions and sampling dates. As in 1987, there was an interaction between fraction and sampling date in 1988 (P = 0.025, Table 4.17). Upper layer leaf was consistantly greater in CP than all other fractions (Table 4.23). A decrease in CP concentration was observed for ULL, ULS, and LLL over time but LLS CP remained relatively constant among sampling dates. Regardless of layer, leaf CP concentration was always greater than stem CP. There was a layer by sampling date interaction (P = 0.007) for LG herbage CP concentration (Table 4.17). Upper layer CP concentration tended to decrease over time but was always greater than LL CP. As in 1987, whole canopy LG CP concentration was

Table 4.22. Total green herbage crude protein concentration for canopy layer and whole canopy 5-wk limpograss pasture regrowth during mid-summer to early fall in 1988.

Canopy component	Sampling Date			
	28 July	17 Aug.	7 Sept.	28 Sept.
	---------- g kg^{-1} ----------			
Layer				
UL	104[+‡]	85	72	68
LL	54[‡]	47	38	43
SE[§]	2.4	5.7	3.0	2.4
Whole canopy				
	73[¶]	61[¶]	49	52[¶]
SE[#] (1.83)				

[+] The magnitude of the difference between layers within a sampling date differed from that on 7 September ($P \leq 0.05$).
[‡] Date mean within layers differed from that on 7 September ($P \leq 0.05$).
[§] Standard error of the mean.
[¶] Mean differed from that on 7 September ($P \leq 0.05$).
[#] Standard error for whole canopy sampling date means.

Table 4.23. Liapograss herbage crude protein concentration for canopy fraction, layer, and whole canopy 5-wk limpograss pasture regrowth in 1966

Canopy component	Sampling Date			
	26 July	17 Aug.	7 Sept.	26 Sept.
	g kg^{-1}			
Fraction				
ULL	132a*‡	126a	110a	102a‡
ULS	70c‡	56c	46c	41c
LLL	107b‡	96b	87b	92b
LLS	39d	36d	31d	35c
SE	4.5	6.7	4.5	3.2
Layer				
Upper	103x§¶#	83x	70X	66x
Lower	51y#	44y	36y	42y
SE	3.3	7.6	4.5	3.6
Whole canopy§				
(4.0)‡‡	66++	57	45	47

* Fraction means within dates followed by the same letter are not different at the 0.05 level by DMRT.
‡ Date mean within fractions differed from that on 7 September ($P \leq 0.05$).
§ Layer means within dates followed by the same letter are not different ($P \leq 0.05$).
¶ The magnitude of the difference between layers within a sampling date differed from that on 7 September ($P \leq 0.05$)
\# Date mean within layers differed from that on 7 September ($P \leq 0.05$).
++ Mean differed from that on 7 September ($P \leq 0.05$).
‡‡ Standard error for whole canopy date means.
SE Standard error of the mean.

greatest for the first sampling date and tended to be lowest for 7 September.

Total green herbage CPBD was affected by a sampling date by canopy layer interaction (P = 0.013, Table 4.4). Crude protein bulk density for 7 September UL (59 g m^{-3}) and LL (99) were lower than for 28 July UL and LL (92 and 126, respectively) and for 28 September LL (134) (Table 4.24). With the exception of the first sampling date, LL CPBD tended to increase over the season. Whole canopy CPBD was higher for the first sampling date (103) than for 7 September (76), but whole canopy CPBD for the other two sampling dates was not different than for 7 September (Table 4.24).

Discussion

It has been suggested by Hennetje and Ebersohn (1980) that the establishment of causal relationships between animal production (performance) and pasture attributes is dependent upon defining pasture attributes in terms fundamental to intake. Theories on intake-control have been described by Conrad (1966) which include distention and chemostatic mechanisms operating to control intake. More recently, ingestive behavior (e.g. bite weight) has been recognized as another important intake-controlling mechanism (Hodgson, 1985) and has been shown to be related to sward canopy structure (Allden and Whittaker, 1970; Stobbs, 1973a). Moore

Table 4.24. Total green herbage crude protein bulk density for canopy layer and whole canopy 5-wk limpograss pasture regrowth during mid-summer to early fall in 1988

Canopy component	Sampling Date			
	28 July	17 Aug.	7 Sept	28 Sept.
	g m^{-3}			
Layer				
UL	92†‡	67	59	60
LL	126‡	80	99	134‡
SE§	8.5	3.7	7.0	11.5
Whole canopy				
(5.3)#	103¶	72	76	92

† The magnitude of the difference between layers within a sampling date differed from that on 7 September ($P \leq 0.05$)
‡ Date mean within layers differed from that on 7 September ($P \leq 0.05$).
§ Standard error of the mean.
¶ Mean differed from that on 7 September ($P \leq 0.05$).
# Standard error for whole canopy sampling date means.

(1983) has elaborated on pasture attributes that interplay with these control mechanisms and illustrated the complexity of their interrelationships. In the current study, LG pastures were characterized in an effort to determine what pasture attributes may have contributed to the depression in animal performance that was observed (Chapter III)

Although botanical composition tended to vary between layers and changed over time, there was no indication that botanical composition was related to changes in animal performance on LG pastures. Steer ADG was highest during the latter part of the season in both years, the time when the proportion of dead material in the sward canopy tended to be greatest. Marthras and Grant (1984) reported that sheep were less likely to graze basal layers of a grass sward canopy that contained dead material. In the current study, percentage of dead material in the upper layer was 5% or less except on the last date of 1987. Because of the relatively tall stubble height at the end of a grazing period, cattle likely were able to avoid the majority of the dead herbage in the canopy.

Grazing animals show a preference for leaf over stem material and, when given the opportunity, will select leaf (Arnold, 1980; Chacon and Stobbs, 1976; Poppi et al., 1980). Limpograss LSR was consistently higher in the upper canopy layer and the ratio within layers remained relatively constant after the first period of the season when it was

highest. The high proportion of stem observed in the lower canopy layer was consistent with earlier reports (Rueland et al., 1988; Sollenberger et al., 1988a; Sollenberger et al., 1989). Chacon and Stobbs (1976) have suggested that selective grazing for leaf can be a nutritional disadvantage, particularly in swards where there is a high degree of vertical variability in LSR. As described by Minson (1983), this disadvantage is related to the grazing animal becoming accustomed to eating the leaf fraction at the top of the canopy and then continuing to select for leaf even though very little may be present in the lower canopy. The potential for this phenomenon exists in rotationally-grazed LG where UL LSR was three to six times higher than in LL. Our data do not suggest that low steer gains measured on 4 Aug. 1987 and 7 Sept. 1988 were due to a reduction in whole canopy LSR, however, because LSR was similar over the last 63 d of the season.

Dry matter bulk density was lower in the upper half of the canopy than in the lower half. Moore et al. (1987) reported that total bulk density of a LG-aeschynomene association increased from the top to the base of the canopy primarily because LG bulk density was greatest at the base. Whole canopy bulk density increased over time, but UL DMBD remained relatively constant and the increase in whole canopy bulk density was primarily due to an increase in the LL. Stobbs (1973b) reported that basal layers of Setaria anceps

and Chloris gayana swards had higher total bulk density than did upper layers, but leaf density was very low in basal layers and this leaf was generally inaccessible to grazing animals. Moore et al. (1987) observed a negative relationship (r = -0.55) between bite weight and canopy bulk density, and this may have been important in the current study when canopies were tall and a relatively large proportion of the LL was included in the grazed portion of the canopy.

Changes over the season in canopy height were different between 1987 and 1988. In 1987, canopy height of 5-wk regrowth tended to decline over the season whereas in 1988 canopy height was higher during the middle of the season than at the beginning or end. Short canopies at the beginning of the 1988 season were due to drought stress and slow growth rates. Allden and Whittaker (1970) reported that the bite size of sheep grazing 'Wimmera' ryegrass (Lolium rigidum Gaud.) increased with increasing tiller length. Working with tropical grasses, Stobbs (1973a) reported that bite size was lower for cattle grazing tall, stemmy Digitaria decumbens and Chloris gayana (induced with gibberallic acid treatment) than for those grazing the same species that had been treated with 2-chloroethyl-trimethylamine chloride to stunt growth and shorten internode length. Our data showed that low gains coincided with periods when canopy height, hence LG growth

rate and possibly physiological maturity, was greater relative to periods of shorter canopy height.

Similar to previous reports (Rusland et al., 1988), we observed no clear relationship between seasonal trends in IVDOM concentration and ADG. The range in total green herbage IVDOM for UL during 1987 and 1988 seasons was similar to that reported by Rusland et al. (1988) for hand-plucked herbage. It was somewhat surprising to observe higher IVDOM concentration for ULS than for leaf blade in both years. This may have been due to the fact that stem in the UL was actively growing and elongating and had yet to develop large amounts of secondary wall thickening which has been shown to adversely affect digestibility (Schank et al., 1973). Highly digestible sheath associated with the stem material might have also contributed to the overall higher digestibility of the ULS fraction.

Overall CP concentration for total green herbage in 1987 appeared to be lower than in 1988. This was partially due to a higher LG LSR in 1988. In both years, whole canopy CP concentration was lowest during the time of the season when lowest ADG was observed. In 1987, UL green herbage CP concentration was lower at the second sampling date than for the first and third dates, but no sampling date differences were detected for LL CP. Both UL and LL CP concentration were higher for the first than the third period of 1988, and

third period CP tended to be lower for both layers than that at other dates except for the fourth period UL.

Recent pasture studies have demonstrated that LG CP concentration is generally low (Sollenberger et al., 1987b; Rusland et al., 1988; Sollenberger et al., 1989). Our results indicate that the low CP concentration observed in LG herbage is due to the combined effect of low CP concentration of stem and its large contribution to total herbage mass. Stem and sheath represented approximately 77% of pre-graze herbage mass in the LG sward canopy in both years and LLS CP concentration averaged 30 to 35 g kg^{-1}.

Due to the erect growth habit of LG, plant material at the top of the canopy is not as mature as at the base. Higher CP (as well as IVDOM) concentration in ULL compared to LLL was most likely related to maturity difference. As leaves mature, N tends to be exported to regions of active growth, resulting in a net loss of N in mature plant parts (Mae and Ohira, 1982; Simpson, 1986).

There are numerous reports in the literature describing the decline in CP concentration with advancing maturity of both tropical (Milford and Haydock, 1965; Oalnum and Dirven, 1972) and temperate (Wilman and Wright, 1978) grasses. Assuming that UL herbage was entirely new growth for each sampling date in the current study, the UL herbage would be of approximately the same maturity for each sampling date. Therefore, fluctuations observed in UL LG herbage CP

concentration over sampling dates were likely due to factors other than advancing maturity. Abdalla et al. (1988b) observed seasonal variation in hand-plucked CP concentration of rotationally-grazed bromegrass (Bromus inermis Leyss.) and attributed this to changes in percentage leaf. Our results show that differences in UL LSR help to explain sampling date variation in UL CP concentration, particularly between the first and second sampling dates. Variation among dates 2 through 4, however, cannot be accounted for simply by changes in UL LSR alone.

Variation in canopy height among periods and the manner in which canopies were stratified during sampling affected the composition of layers. As a result, the relative contribution of UL and LL to steer diets was not consistent over periods. Lispograss pastures were consistently grazed to a 20-cm stubble height. Therefore, as canopy height increased, the relative contribution of what was defined as LL herbage to the animal's diet likely increased proportionately. For example in 1987, canopy height was 55 cm (60 cm when the 5-cm stubble was included) for 4 August. Consequently, UL and LL each represented approximately 28 cm of the canopy. If grazed to a 20-cm stubble and assuming the entire UL was removed, then approximately 43% (12 cm) of the total height of the lower canopy layer was also consumed. For the last sampling date in 1987, canopy height was 42 cm. When UL was removed by grazing, only 8 cm (or 29%) of the

lower canopy layer remained before grazing was discontinued at the 20-cm stubble height. Despite LSR within UL and LL being similar for the last 63-d of each grazing season, this implies that LSR of the herbage consumed may have been greater when canopies were shorter (periods 3 and 4 in 1987; period 4 in 1988) because less of the LL was grazed. In addition, CP concentration of LL, which was expected to be higher in taller pastures because of a greater percentage of new regrowth (versus old stubble) in layer DM, was or tended to be lower during the slump periods. So, if steers were consuming more of this layer when pastures were tall, CP of herbage consumed could have been lower than the layer data might suggest. These two factors, LSR and plant part CP concentration, appear to play a major role in limiting CP concentration of LG herbage consumed by grazing cattle.

Summary and Conclusions

A study was conducted to identify and describe changes in canopy structure and forage nutritive value of LG pasture and to make inferences about forage and pasture attributes that may be contributing to the summer slump. Dividng the sward canopy into layers provided for a more descriptive assessment of LG pasture than did whole canopy data. No single pasture attribute or forage component, however, could be identified as the most important factor contributing to

the summer slump condition. There was no indication that botanical composition, DM bulk density, or IVDOM concentration of LG pasture contributed to the low animal performance that was observed during specific periods in each of the two grazing seasons.

Of the forage and pasture attributes assessed in this study, leaf and stem distribution and CP concentration appeared to be related to the slump in animal performance that was observed on LG pasture. Low CP concentration and the proportion of leaf blade in the grazed portion of the canopy, particularly when canopies were tallest, may have reduced intake and steer gains on LG pasture.

CHAPTER V
CHARACTERIZATION OF NITROGEN FORM AND DISTRIBUTION IN A LIMPOGRASS SWARD CANOPY

Introduction

Many tropical grass species used as forage crops are of inherently low nutritive value, particularly with respect to crude protein (CP) concentration (Moore and Mott, 1973; Wilson and Minson, 1980). For ruminant animals, dietary CP concentrations that are below 70 g kg^{-1} are believed to limit animal performance (Minson and Milford, 1967), and may be lower than the minimum level required for a positive N balance (Milford and Haydock, 1965). Florelta' limpograss [Hemarthria altissima (Poir.) Stapf et C.E. Hubb.] pasture has been found to be marginal in meeting the CP requirement for growing steers (Rusland et al., 1988).

Measurement of total N concentration (expressed as CP) of whole canopy samples has traditionally been used to at least partially describe the relative nutritive value of pasture forage. Actual CP availability, however, can vary considerably from observed CP concentrations (NRC, 1985). The partitioning of plant N into neutral and acid detergent soluble and insoluble portions has been used to estimate the relative degradability of various N fractions (Abdalla et

al , 1998a; Sanderson and Wedin, 1999a). This has been primarily in response to the current emphasis on distinguishing between ruminally degradable and undegradable protein as well as indigestible protein in feeds (Pichard and Van Soest, 1977; NRC, 1985).

Variation in N concentration of plant material by plant part and maturity has been well documented in the literature. Nitrogen concentration (hence, CP concentration) of leaf material is generally higher than that of stems and petioles, and younger plant material often has higher N concentration than more mature herbage (Minson, 1971). Due to the relatively high percentage of stem in many tropical grasses (Wilson and Minson, 1980; Sollenberger et al., 1988a), greater anatomical and compositional variability can occur vertically through the sward canopy of tropical grasses ('t Mannetje and Ebersohn, 1980; Stobbs, 1973b) than with temperate species. There is also potential for variability in N content throughout the grass canopy depending on the relative proportions of leaf and stem material and their respective N concentrations at different levels within the canopy.

Therefore, a more descriptive assessment of forms of forage N, particularly of tropical forage grasses that are low in N concentration, may be warranted. The objectives in this 2-yr study were to characterize seasonal changes in the

distribution of N, and to describe and quantify forms of N in a rotationally-grazed limpograss pasture.

Materials and Methods

The experiment was conducted in 1987 and 1988 at the Forage Evaluation Field Laboratory of the Beef Research Unit near Gainesville, Florida. Floralta limpograss pastures used in this study were part of a concurrent animal grazing study and a description of the pastures and their management was given in Chapter III. Sampling procedures and sample preparation for limpograss herbage was described in Chapter IV.

All limpograss fractions, i.e., upper layer leaf (ULL), upper layer stem (ULS), lower layer leaf (LLL), and lower layer stem (LLS) samples were analyzed for NDF, NDFN, ADF, and ADFN. A modified aluminum block digestion procedure (Gallahar et al., 1975) and semi-automated colorimetry (Hambleton, 1977) were used for all N determinations including appropriate standards and blanks.

Neutral detergent fiber-N was determined by refluxing the sample in neutral detergent solution as described by Goering and Van Soest (1970). The fiber residue was collected by filtration through Whatman Reeve Angle 802 filter paper of known dry weight, washing the residue with hot distilled water and rinsing with acetone. The NDF

residue plus filter paper was dried (105°C) and weighed. Neutral detergent fiber concentration (DM basis) was calculated as the ratio of NDF residue DM (minus filter paper) to initial sample DM. Nitrogen in the NDF residue plus filter paper was determined as described above. Acid detergent fiber (DM basis) and ADFN were determined in a similar manner using acid detergent solution as described by Goering and Van Soest (1970).

In 1988, non-protein N (NPN) was determined by refluxing the sample in distilled water (i.e., hot-water extraction) according to Goering and Van Soest (1970). A modification was made in the procedure whereby true protein in the hot water filtrate was quantified using a procedure based on the Bradford Method (Bradford, 1976) which utilizes the principle of protein-dye binding. The filtrate from each hot water extract was collected in a vacuum flask, cooled to room temperature and brought to volume in a 500-ml volumetric flask. A 15-ml aliquot was taken from the filtrate and stored at 4.5°C until assayed for protein. A commercial Coomassie Blue G-250 protein assay reagent (Pierce Chemical Co., Rockford, Ill.) was used according to the manufacturer's specifications. One milliliter of protein assay reagent was added to 1 ml of the sample aliquot, vortexed, and absorbance was read at 595 nm. A standard curve was prepared using a stock bovine serum albumin standard dilution series in a range of 1 to 25 ug ml^{-1}. Non-protein N was estimated as the

difference between total N and hot water extract residue N and adjusted for the quantity of true protein in the hot water filtrate, as determined by protein assay. Cell contents (non-cell wall) true protein N (CCTPN) was estimated as the difference between hot water extract residue N plus true protein N in the hot water filtrate and NDFN.

Nitrogen content is expressed as g m^{-2}. Neutral detergent fiber, NDFN, ADF, and ADFN concentration are expressed on a DM basis. Nitrogen in NDF and ADF is also expressed as a percentage of total N (NDFNTN and ADFNTN, respectively). Non-protein N (NPNTN) and cell contents (non-cell wall) true protein N (CCTPNTN) for 1988 are expressed as a percentage of total N.

Response variables were also determined on a layer and whole canopy basis by calculating the sum of weighted contributions of respective fractions. For example, upper layer NDF concentration is calculated as the sum of ULL and ULS NDF content divided by the combined weight of ULL and ULS herbage mass.

The experimental design was completely randomized with 6 and 4 replications in 1987 and 1988, respectively. Statistical analyses were performed separately for canopy fractions (ULL, ULS, LLL, and LLS), canopy layers (upper and lower), and for whole canopy data. Repeated measures (sampling date) analysis of variance procedures were used. Statistics are based on the univariate approach with degrees

of freedom correction. Mean comparisons of canopy fractions within sampling dates were by Duncan's multiple range test (DMRT) when appropriate. Comparisons of fraction means over sampling dates when appropriate ($P \leq 0.05$) were made using appropriate single degree of freedom contrasts, due to restrictions imposed by repeated measures analysis. Among sampling date comparisons (when appropriate) were done with preplanned contrasts. Contrasts used compared the second sampling date in 1987 and the third sampling date in 1988 with each of the other three dates within years.

Results

Nitrogen distribution: 1987

There was a canopy fraction by sampling date interaction ($P = 0.010$, Table 5.1) for N content (TN; expressed as g m^{-2}). The greatest amount of N was in LLS for all sampling dates except the first (Table 5.2). For the first sampling date (15 July) N content for ULL, ULS, and LLS was not different. Leaf in the LL tended to have the least N throughout the season, but was not different from ULL and ULS at dates 2 through 4. The combined N content of fractions within layers indicates that only for the first sampling date did total N content for the UL (3.1 g m^{-2}) exceed that of the LL (2.6). For the last three sampling dates there tended to

Table 5.1 Levels of probability for differences in response variables due to limpograss canopy fraction (F), canopy layer (L), sampling date (D), and their interactions, and whole canopy analysis by sampling date in 1987.

	Response Variables						
Effect	TN	NDF	NDFN	NDFNTN	ADF	ADFN	ADFNTN
Canopy Fraction Analysis:							
F	***	***	***	0.006	***	***	***
D	0.046	***	0.021	0.006	***	0.146	0.006
F X D	0.010	0.003	0.091	0.343	0.306	0.166	0.043
Canopy Layer Analysis:							
L	0.204	***	***	0.016	0.001	0.394	***
D	0.053	***	0.670	0.017	***	0.015	0.042
L X D	0.002	0.752	0.756	0.366	0.346	0.262	0.034
Whole Canopy Analysis:							
D	0.106	0.003	0.615	0.072	0.065	0.036	0.341

*** $P < 0.001$.

Table 5.2. Canopy fraction total N content of 5-wk limpograss regrowth in 1987.

Canopy component	Sampling Date: 15 July	4 Aug.	25 Aug.	16 Sept.
	g m^{-2}			
Fraction				
ULL	1.3a+	0.9b	1.1b	0.9b
ULS	1.7a‡	1.0b	1.1b	1.0b
LLL	0.5b	0.7b	0.5b	0.6b
LLS	2.1a	2.5a	2.1a	2.0a
SE	0.34	0.30	0.27	0.22
Layer				
Upper	3.1x§¶#	1.9y	2.2x¶	1.6y
Lower	2.6x	3.2x	2.6x	2.7x
SE	0.59	0.48	0.46	0.41
Whole canopy				
	5.7	5.0	4.8	4.4 NS

+ Fraction means within dates followed by the same letter are not different at the 0.05 level by DMRT.
‡ Date mean within fractions differed from that on 4 August ($P \leq 0.05$).
§ Layer means within dates followed by the same letter are not different ($P \leq 0.05$)
¶ The magnitude of the difference between layers within a sampling date differed from that on 4 August ($P \leq 0.05$).
# Date mean within layer differed from that on 4 August ($P \leq 0.05$).
SE Standard error of the mean.

ba or was more N in the LL. The amount of N in LLS represented 36, 50, 43, and 44% of total canopy N within each of the respective sampling dates. On a layer basis, N content in the UL was greater for the first sampling date than for the second. Lower layer N content did not differ among sampling dates. Whole canopy N content did not differ among sampling dates ($P = 0.109$, Table 5.1) but tended to decrease over time.

Neutral detergent fiber nitrogen concentration: 1987

There was an interaction ($P = 0.003$) between fraction and sampling date for NDF concentration (Table 5.1). Upper layer leaf had the lowest NDF concentration of all fractions, but it did not differ between sampling dates, averaging 686 g kg^{-1} DM (Table 5.3). Lower layer stem had the greatest NDF concentration, and it tended to increase over time. In general, sampling date tended to have a greater effect on NDF concentration in stem than in leaf. Layers differed in NDF concentration such that UL was less than LL. On a whole canopy basis, NDF concentration increased over time from 788 g kg^{-1} on the first date to 823 g kg^{-1} for the last sampling date.

Sampling date did not affect NDFN on either a layer, or whole canopy basis (Table 5.1). Fractions differed in NDFN such that ULL > LLL > ULS > LLS over sampling dates (Table

Table 5.3 Canopy fraction, layar, and whole canopy neutral detergent fiber concentration of 5-wk limpograss regrowth in 1987.

Canopy component	Sampling Date: 15 July	4 Aug	25 Aug.	16 Sept	
	g kg^{-1} DM				
Fraction					
ULL	686d[+]	679d	686d	693d	
ULS	782b[‡]	800b	804b	819b	
LLL	716c[‡]	701c	709c	728c[‡]	
LLS	820a	831a	832a	853a[‡]	
SE	9.9	5.1	6.6	9.6	
Layer					Mean
Upper	755	774	773	787	772[§]
Lower	809	820	823	841	823 (5.3)[¶]
Mean (5.1)[¶]	782[++]	797	798	814[++]	
Whole canopy					
(6.2)[§§]	788[‡‡]	807	805	823[‡‡]	

[+] Fraction means within dates followed by the same letter are not different at the 0.05 level by DMRT.
[‡] Data mean within fractions differed from that on 4 August ($P \leq 0.05$).
[§] Layer means over dates differed ($P \leq 0.05$).
[¶,#] Standard errors for layer means over dates and date means over layers, respectively.
[++] Data mean over layers differed from that on 4 August ($P \leq 0.05$).
[‡‡] Mean differed from that on 4 August ($P \leq 0.05$).
[§§] Standard error for whole canopy data means.
SE Standard error of the mean

Table 5.4. Canopy fraction, layer, and whole canopy neutral detergent fiber (NDF) N concentration of 5-wk limpograss regrowth in 1987.

Canopy component	Sampling Date: 15 July	4 Aug.	25 Aug.	16 Sept.	Mean	Contrast+: ULL	ULS
	g N kg^{-1} NDF						
Fraction							
ULL	12.4	14.7	14.0	13.9	13.7		
ULS	5.2	5.2	5.3	4.9	5.2		
LLL	9.7	13.3	13.8	13.6	12.6	*	***
LLS	4.1	4.0	4.3	4.0	4.1		*
Mean	7.8¶	9.3	9.4	9.1	(0.53)‡		
(0.47)§							
Layer							
Upper	7.6	7.4	7.5	6.9	7.4#		
Lower	4.6	4.6	5.0	4.6	4.7		
					(0.24)++		
Whole canopy							
	5.7	5.4	5.8	5.4	NS		

*,***,NS P ≤ 0.05 and 0.001 and P > 0.05, respectively.
+ Preplanned single df contrasts to test differences in fraction over date means.
‡,§ Standard errors for fraction means over dates and date means over fractions, respectively.
¶ Date mean over fractions differed from that on 4 August (P ≤ 0.05).
# Layer means over dates differed at the 0.05 level.
++ Standard error for layer means over dates

5.4). Neutral detergent fiber N concentration appeared to deviate more between plant parts (leaf and stem) than layers, although UL NDFN was higher than that of LL. Leaf NDFN was 2 to 3 times greater than stem NDFN, whereas UL NDFN was approximately 1.5 times greater than LL NDFN. Whole canopy NDFN averaged 5.6 g kg^{-1}. Sampling date means for the by fraction analysis are presented for comparison to actual whole canopy means. The relative difference between sampling date NDFN means (over fractions) and whole canopy means is due to the weighted contribution of individual fractions in calculating whole canopy NDFN.

Differences in NDFNTN (g NDFN kg^{-1} N) were due to fraction and sampling date but not their interaction (Table 5.1). There was no difference in NDFNTN between ULL (612), ULS (645), and LLL (645; Table 5.5). Lower layer stem was greater in NDFNTN (715) than was ULS. Highest NDFNTN was observed on 4 August. Layers differed in NDFNTN, in that UL (628) was less than LL (699). Whole canopy NDFNTN did not differ between sampling dates ($P = 0.072$; Table 5.1), but it tended to be highest on 4 August. When analyzed on a canopy fraction or layer basis, NDFNTN was greatest for 4 August.

Acid detergent fiber nitrogen concentration: 1987

Acid detergent fiber concentration (DM basis) decreased over time within each fraction and layer, and tended to

Table 5.5. Canopy fraction, layer, and whole canopy neutral detergent fiber N (NDFN) as a percentage of total N of 5-wk limpograss regrowth in 1967.

Canopy component	Sampling Date: 15 July	4 Aug.	25 Aug.	16 Sept	Mean	Contrast+: ULL	ULS
	----- g NDFN kg^{-1} total N ------						
Fraction							
ULL	580	654	600	614	612		
ULS	635	733	656	657	645		
LLL	590	660	666	662	645	NS	NS
LLS	665	746	734	693	715		**
Mean (19.8)§	596¶	699	664¶	656¶	(25.9)‡		
Layer							
Upper	546	696	630	636	626#		
Lower	655	727	720	664	699		
Mean (28.0)‡‡	606§§	712	675	660§§	(25.4)++		
Whole canopy	603	715	676	660	NS		

**,NS $P \leq 0.01$ and $P > 0.05$, respectively.
+ Preplanned single df contrasts to test differences in fraction means over dates.
‡,§ Standard errors for fraction means over dates and date means over fractions, respectively.
¶ Date mean over fractions differed from that on 4 August ($P \leq 0.05$).
# Layer means over dates differed ($P \leq 0.05$).
++,‡‡ Standard errors for layer means over dates and date means over layers, respectively.
§§ Date mean over layers differed from that on 4 August ($P \leq 0.05$).

decrease on a whole canopy basis (Tables 5.1 and 5.6). Over sampling dates, ADF concentration was highest for LLS (418 g kg^{-1} DM) and lowest for ULL (369). Acid detergent fiber concentration for ULS and LLL were similar and averaged 386 g kg^{-1}.

No interaction between fraction and sampling date was observed for ADFN (P = 0.196, Table 5.1). Nitrogen concentration in ADF tended to be higher in leaf material than in stem and this difference was similar within both layers (Table 5.7). There was no difference in ADFN between layers, and the mean was 2.3 g N kg^{-1} ADF. Sampling date effects on ADFN were similar between layers and for whole canopy in that ADFN was higher for the first and third sampling date than for the second sampling date.

Acid detergent fiber N expressed as a percentage of total N (g ADFN kg^{-1} N) was effected by a fraction by sampling date interaction (P = 0.043, Table 5.1). Lower layer stem was consistently higher in ADFNTN than any other fraction within each sampling date. For the first sampling date, ADFNTN did not differ among ULL, ULS, and LLL, however, over the last three dates, ULS ADFNTN was greater than ULL and LLL, averaging 75, 121, and 88 g ADFN kg^{-1} N, respectively (Table 5.8). Acid detergent fiber N as a percentage of total N tended to be highest for all fractions for the first sampling date. The highest ADFNTN was observed for LLS on 15 July when approximately 21% of LLS total N was

Table 5.6. Canopy fraction, layer, and whole canopy acid detergent fiber concentration of 5-wk limpograss regrowth in 1987.

Canopy component	Sampling Date: 15 July	4 Aug.	25 Aug	16 Sept.	Mean	Contrast+: ULL	ULS
	g kg^{-1} DM						
Fraction							
ULL	393	366	363	354	369		
ULS	408	386	378	366	385		
LLL	417	378	375	382	388	**	NS
LLS	428	417	414	412	418		***
Mean	412¶ (4.4)§	387	382	378¶	(7.0)‡		
Layer							
Upper	404	381	374	363	380#		
Lower	427	414	410	409	415		
Mean	416§§ (6.2)‡‡	398	392	386§§	(7.4)++		
Whole canopy	418	406	388	394	NS		

,*,NS $P \leq 0.01$ and 0.001 and $P > 0.05$, respectively.
+ Preplanned single df contrasts to test differences in fraction means over dates.
‡,§ Standard errors for fraction means over dates and date means over fractions, respectively.
¶ Date mean over fractions differed from that on 4 August ($P \leq 0.05$).
# Layer means over dates differed at the 0.05 level.
++,‡‡ Standard errors for layer means over dates and date means over layers, respectively.
§§ Date mean over layers differed from that on 4 August ($P \leq 0.05$).

Table 5.7. Canopy fraction, layer, and whole canopy acid detergent fiber N concentration of 5-wk limpograss regrowth in 1987.

Canopy component	Sampling Date: 15 July	4 Aug.	25 Aug.	16 Sept.	Mean	Contrast[+]: ULL	ULS
	g N kg^{-1} ADF						
Fraction							
ULL	3.3	3.2	3.2	3.3	3.2		
ULS	2.0	1.8	2.1	2.0	2.0		
LLL	3.1	3.2	3.6	3.5	3.4	NS	***
LLS	2.4	2.0	2.2	1.9	2.1		NS
					(0.13)[‡]		
Layer							
Upper	2.4	2.1	2.4	2.3			
Lower	2.5	2.0	2.3	2.0			
Mean (0.12)[¶]	2.4[§]	2.0	2.4[§]	2.2			
Whole canopy							
(0.14)[#]	2.5[++]	2.1	2.4[++]	2.1			

***,NS P ≤ 0.001 and P > 0.05, respectively.
[+] Preplanned single df contrasts to test differences in fraction means over dates.
[‡] Standard error for fraction means over dates.
[§] Date mean over layers differed from that on 4 August (P ≤ 0.05).
[¶] Standard error for date means over layers.
[#] Standard error for whole canopy date means.
[++] Date mean differed from that on 4 August (P ≤ 0.05).

Table 5.8. Canopy fraction, layer, and whole canopy acid detergent fiber N (ADFN) as a percentage of total N of 5-wk limpograss regrowth in 1987

Canopy component	Sampling Date			
	15 July	4 Aug.	25 Aug.	16 Sept.
	------ g ADFN kg^{-1} total N ------			
Fraction				
ULL	98b[+]	78c	72d	78c
ULS	105b	116b	125b	121b
LLL	121b‡	85c	91c	89c
LLS	209a	183a	186a	180a‡
SE	19.7	12.5	8.7	11.7
Layer				
Upper	98y[§]	97y	101y	100y
Lower	199x¶	182x	187x	143x
SE	12.6	13.4	8.4	11.8
Whole canopy				
	141	139	137	124 NS

[+] Fraction means within dates followed by the same letter are not different at the 0.05 level by DMRT.
‡ Date mean within fractions differed from that on 4 August ($P \leq 0.05$).
§ Layer means within dates followed by the same letter are not different ($P \leq 0.05$).
¶ Date mean within layers differed from that on 4 August ($P \leq 0.05$).
SE Standard error of the mean.
NS $P > 0.05$.

associated with ADF. Whole canopy ADFNTN did not differ among sampling dates ($P = 0.341$, Table 5.1) and averaged 135 g kg^{-1}.

Nitrogen distribution; 1988

There was an interaction between fraction and sampling date for N content (g m^{-2}; $P < 0.001$, Table 5.9). Between fraction differences in N content varied with sampling date although overall trends were similar to 1987 (Table 5.10). Stem in the LL had the highest N content of all fractions except ULL on 28 July and represented a large proportion of whole canopy N content. Lower layer stem N content represented 32, 38, 47, and 50% of that in the total canopy for the first through last sampling dates, respectively. Leaf contributed more than 50% of the N content of the UL. As in 1987, LLL N content in 1988 varied little between sampling dates. Within each of the first two sampling dates, UL and LL did not differ in N content. Upper layer N content was less than LL for each of the last two sampling dates. On a whole canopy basis, N content was generally higher for the middle two sampling dates than for either the first or last dates.

Table 5.9. Levels of probability for differences in response variables due to limpograss canopy fraction (F), canopy layer (L), sampling date (D), and their interactions, and whole canopy analysis by sampling date in 1988

	Response Variables								
Effect	TN	NOF	NDFN	NDFNTN	ADF	ADFN	ADFNTN	NPNTN	CCTPNTN
Canopy Fraction Analysis:									
F	***	***	***	0.094	***	***	***	0.314	0.006
D	***	***	***	***	***	***	***	***	***
F X D	***	0.001	***	0.067	***	0.034	0.274	0.749	0.363
Canopy Layer Analysis:									
L	0.004	***	***	0.167	0.041	0.007	***	0.111	0.074
D	0.001	***	***	0.006	***	0.009	***	***	0.014
L X D	0.006	0.154	***	0.931	0.001	0.003	0.133	0.686	0.672
Whole Canopy Analysis:									
D	0.045	0.006	0.001	0.675	0.035	0.299	0.001	0.001	0.089

*** P < 0.001.

Table 5.10. Canopy fraction total N content of 5-wk
limpograss regrowth in 1982.

Canopy component	Sampling Date			
	28 July	17 Aug.	7 Sept.	28 Sept.
	g m^{-2}			
Fraction				
ULL	1.4a[+]	1.7b	1.3b	0.9b[‡]
ULS	0.7b	1.2c	0.9bc	0.5c[‡]
LLL	0.9b	0.9c	0.7c	0.8bc
LLS	1.4a[‡]	2.3a	2.6a	2.2a[‡]
SE	0.15	0.17	0.17	0.14
Layer				
Upper	2.2x[§¶]	2.9x[#]	2.2y	1.4y[#]
Lower	2.3x[#]	3.2x	3.3x	3.0x[#]
SE	0.31	0.30	0.26	0.18
Whole canopy				
(0.40)[‡‡]	4.5[++]	6.1	5.5	4.4[++]

[+] Fraction means within dates followed by the same letter are not different at the 0.05 level by DMRT.
‡ Date mean within fractions differed from that on 7 September ($P \leq 0.05$).
§ Layer means within dates followed by the same letter are not different ($P \leq 0.05$).
¶ The magnitude of the difference between layers within a sampling date differed from that on 7 September ($P \leq 0.05$).
# Date mean within layers differed from that on 7 September ($P \leq 0.05$).
++ Mean differed from that on 7 September ($P \leq 0.05$).
‡‡ Standard error for whole canopy date means.
SE Standard error of the mean.

Neutral detergent fiber nitrogen concentration 1988

For NDF concentration, there was an interaction between fraction and sampling date ($P = 0.001$, Table 5.9). Differences in NDF concentration by fraction, layer, and sampling date were similar to those in 1987 (Table 5.11).

There was an interaction between fraction and sampling date ($P < 0.001$, Table 5.9) for NDFN. Within all fractions, NDFN decreased from the first sampling date to the last (Table 5.12). There was a greater decrease over time in NDFN for ULL and ULS than for leaf and stem, respectively, in the LL. As in 1987, leaf NDF was higher in N concentration than stem. Upper layer leaf NDFN was greater than LLL NDFN within all sampling dates. In the UL, NDFN was approximately twice as high as in the LL for all sampling dates. Whole canopy NDFN was affected by sampling date ($P = 0.001$, Table 5.9) in that NDFN was greater for 28 July than 7 September.

Data for N in NDF expressed as a percentage of total N (NDFNTN) showed no differences among fractions in 1988 although LLS tended to be higher in NDFNTN than other fractions (Table 5.13). Lower canopy layer NDFNTN tended to be higher than for UL. All fractions were highest in NDFNTN for the first sampling date. Whole canopy NDFNTN did not differ among sampling dates and averaged 628 g NDFN kg^{-1} N.

Table 5.11. Canopy fraction, layer, and whole canopy neutral detergent fiber concentration of 5-wk limpograss regrowth in 1988.

Canopy component	Sampling Date 26 July	17 Aug.	7 Sept.	28 Sept.	
	---------- g kg^{-1} DM ----------				
Fraction					
ULL	707c[+]	714d	730c	710c	
ULS	750b[‡]	783b[‡]	816b	817a	
LLL	727c	735c	738c	735b	
LLS	812a[‡]	815a[‡]	836a	832a	
SE	8.1	8.1	8.7	8.2	
Layer					Mean
Upper	727	757	784	774	760[§]
Lower	797	805	827	821	812
Mean (8.1)[¶]	762[++]	781[++]	806	798	(2.8)[§]
Whole canopy					
(7.4)[§§]	774[‡‡]	790[‡‡]	816	810	

[+] Fraction means within dates followed by the same letter are not different at the 0.05 level by DMRT.
[‡] Data mean within fractions differed from that on 7 September ($P \leq 0.05$).
[§] Layer means over dates differed at the 0.05 level.
[¶,#] Standard errors for layer means over dates and date means over layers, respectively.
[++] Data mean over layers differed from that on 7 September ($P \leq 0.05$).
[‡‡] Mean differed from that on 7 September ($P \leq 0.05$).
[§§] Standard error for whole canopy date means.
SE Standard error of the mean.

Table 5.12. Canopy fraction, layer, and whole canopy neutral detergent fiber (NDF) N of 5-wk limpograss regrowth in 1988.

Canopy component	Sampling Date			
	28 July	17 Aug.	7 Sept.	28 Sept.
	g N kg^{-1} NDF			
Fraction				
ULL	19.4a[+‡]	17.3a‡	14.8a	13.6a‡
ULS	9.6c‡	6.8c	5.4c	4.9c
LLL	16.7b‡	12.4b‡	10.0b	11.4b‡
LLS	5.2d	4.6d	3.8d	4.2c
SE	0.67	0.99	0.36	0.48
Layer				
Upper	14.6x[§¶‡]	10.6x‡	8.6x	8.2x
Lower	7.1y‡	5.5y	4.4y	4.9y
SE	0.58	0.81	0.42	0.46
Whole canopy				
(0.44)‡‡	9.4++	7.1	5.4	5.6

+ Fraction means within dates followed by the same letter are not different at the 0.05 level by DMRT.
‡ Date mean within fractions differed from that on 7 September ($P \leq 0.05$).
§ Layer means within dates followed by the same letter are not different ($P \leq 0.05$).
¶ The magnitude of the difference between layers within a sampling date differed from that on 7 September ($P \leq 0.05$).
‡ Date mean within layer differed from that on 7 September ($P \leq 0.05$).
++ Mean differed from that on 7 September ($P \leq 0.05$).
‡‡ Standard error for whole canopy date means.
SE Standard error of the mean.

Table 5.13. Canopy fraction, layer, and whole canopy neutral detergent fiber N (NDFN) as a percentage of total N of 5-wk limpograss regrowth in 1988.

Canopy component	Sampling Date: 28 July	17 Aug.	7 Sept.	28 Sept.	Mean
	g NDFN kg^{-1} total N				
Fraction					
ULL	646	611	612	593	616a†
ULS	646	603	596	614	615a
LLL	708	583	542	568	600a
LLS	677	652	652	624	651a
Mean (14.5)§	669¶	612	600	600	(18.7)‡
Layer					
Upper	646	610	604	600	615x#
Lower	685	634	625	609	638x
Mean (16.5)‡‡	666§§	622	614	604	(14.8)++
Whole canopy	665	623	617	606	NS

† Fraction means over dates followed by the same letter are not different ($P \leq 0.05$).
‡,§ Standard errors for fraction means over dates and date means over fractions, respectively.
¶ Date means over fractions differed from that on 7 September ($P \leq 0.05$).
# Layer means over dates did not differ ($P \leq 0.05$).
++,‡‡ Standard errors for layer means over dates and date means over layers, respectively.
§§ Date mean over layers differed from that on 7 September ($P \leq 0.05$).
NS $P > 0.05$

Acid detergent fiber nitrogen concentration: 1988

Acid detergent fiber concentration differences between fractions were dependent on sampling date ($F < 0.001$, Table 5.9). Lower layer stem ADF concentration remained relatively constant over sampling dates and averaged 408 g kg^{-1} (Table 5.14). Lower layer leaf ADF concentration was greater generally than ULL ADF, but both fractions tended to increase in ADF concentration over time. There was an interaction between layer and sampling date ($F = 0.001$, Table 5.9) in ADF concentration that was due to changes in UL ADF over time while LL ADF remained constant. Upper layer ADF was less than LL ADF for the first and last sampling dates but layers did not differ in ADF concentration for the second and third sampling dates. Whole canopy ADF concentration tended to be lower at the beginning and end of the season than during the middle of the season although sampling date differences were relatively small.

Overall ADFN concentration in 1988 appeared to be greater than in 1987 (Table 5.15). There was an interaction between fraction and sampling date ($F = 0.034$, Table 5.9). Acid detergent fiber N concentration for ULL, ULS, and LLL tended to decrease over time, whereas LLS remained relatively constant and averaged 2.6 g kg^{-1}. As in 1987, leaf ADFN was greater than stem ADFN within both layers. Differences in ADFN concentration between layers were dependent upon

Table 5.14. Canopy fraction, layer, and whole canopy acid detergent fiber concentration of 5-wk limpograss regrowth in 1988.

Canopy component	Sampling Date 28 July	17 Aug.	7 Sept.	28 Sept.
	---------- g kg^{-1} DM ----------			
Fraction				
ULL	358c†‡	364c‡	377b	373b
ULS	380b‡	423a‡	410a	376b‡
LLL	371bc‡	392b‡	407e	397e
LLS	414e	408ab	408e	401a
SE	8.9	7.2	6.4	9.2
Layer				
Upper	369y§¶#	401x	398x	384y#
Lower	406x	406x	408x	400x
SE	8.7	8.1	7.6	10.2
Whole canopy				
(4.1)‡‡	394++	404	406	394++

† Frection means within dates followed by the same letter are not different at the 0.05 level by DMRT.
‡ Date mean within fractions differed from that on 7 September ($P \leq 0.05$).
§ Layer means within dates followed by the same letter are not different ($P \leq 0.05$).
¶ The magnitude of the difference between layers within a sampling date differed from that on 7 September ($P \leq 0.05$).
# Date mean within layers differed from that on 7 September ($P \leq 0.05$).
++ Mean differed from that on 7 September ($P \leq 0.05$).
‡‡ Standard error for whole canopy date means.
SE Standard error of the mean.

Table 5.15. Canopy fraction, layar, and whole canopy acid detergent fiber (ADF) N of 5-wk limpograss regrowth in 1988.

Canopy component	Sampling Data			
	2a July	17 Aug.	7 Sept.	28 Sept.
	g N kg^{-1} ADF			
Fraction				
ULL	4.5a[+]	4.2a	4.0a	3.5a‡
ULS	3.1c‡	2.7b	2.4c	2.2c
LLL	4.0b	3.9a	3.7b	3.5a
LLS	2.5d	2.7b	2.6c	2.8b
SE	0.24	0.30	0.15	0.22
Layer				
Upper	3.8x§¶	3.2x	3.0x	2.7x¶‡
Lower	2.8y	2.9x	2.7x	2.9x
SE	0.20	0.27	0.27	0.12
Whole canopy				
	3.1	3.0	2.8	2.8 NS

\+ Fraction means within dates followed by the same latter are not different at the 0.05 level by DMRT.
‡ Date mean within fractions differed from that on 7 September ($P \leq 0.05$).
§ Layer means within dates followed by the same letter are not different ($P \leq 0.05$).
¶ The magnitude of the difference between layers within a sampling date differed from that on 7 September ($P \leq 0.05$).
‡ Date mean within layers differed from that on 7 September ($P \leq 0.05$).
NS $P > 0.05$.

sampling date (P = 0.003, Table 5.9). Within the upper canopy layer, ADFN decreased from the first (3.8 g kg^{-1}) to last (2.7) sampling date. Lower layer ADFN was not different between sampling dates and averaged 2.8 g kg^{-1}. Acid detergent fiber N concentration on a whole canopy basis did not differ between sampling dates and averaged 2.9 g kg^{-1}.

There was no interaction between fraction and sampling date for ADFNTN (P = 0.274, Table 5.9) but fraction (P < 0.001) and sampling date (P < 0.001) means differed. Fraction effects were much greater than sampling date effects. Lower layer stem ADFNTN (202 g ADFN kg^{-1} N), over sampling dates, was greater than ULS (127), ULL (83), and LLL (99; Table 5.16). Lower layer ADFNTN (173 g ADFN kg^{-1} N) was greater than that in the upper canopy layer (100). The effect of sampling date on ADFNTN was similar for fractions, layers, and the whole canopy in that there was a general increase in ADFNTN from the first to the third sampling date.

Cell content nitrogen: 1988

Fractions did not differ in NPNTN among sampling dates and averaged 197 g NPN kg^{-1} total N (Table 5.17). There was an increase in NPNTN for all fractions, layers, and the whole canopy from the first through last sampling date such that NPNTN was approximately twice as great for the last sampling date compared to the first

Table 5.16. Canopy fraction, layer, and whole canopy acid detergent fiber N (ADFN) as a percentage of total N of 5-wk limpograss regrowth in 1988.

Canopy component	Sampling Date: 28 July	17 Aug	7 Sept	28 Sept	Mean	Contrast+: ULL	ULS
	----- g ADFN kg^{-1} total N ------						
Fraction							
ULL	77	79	89	87	83		
ULS	108	129	139	133	127		
LLL	88	101	113	95	99	*	**
LLS	172	206	223	206	202		***
Mean (4.7)§	111¶	129¶	141	130	(6.9)‡		
Layer							
Upper	87	100	110	104	100#		
Lower	140	177	197	177	173		
Mean (6.8)‡‡	114§§	138	154	140	(5.9)++		
Whole canopy							
(8.1)¶¶	114##	140	162	153			

*, **, *** P ≤ 0.05, 0.01 and 0.001, respectively
+ Preplanned single df contrasts to test differences in fraction means over dates.
‡, § Standard errors for fraction means over dates and date means over fractions, respectively.
¶ Date mean over fractions differed from that on 7 September (P ≤ 0.05).
# Layer means over dates differed (P ≤ 0.05).
++, ‡‡ Standard errors for layer means over dates and date means over layers, respectively.
§§ Date mean over layers differed from that on 7 September (P ≤ 0.05).
¶¶ Standard error for whole canopy date means.
Mean differed from that on 7 September (P ≤ 0.05).

Table 5.17. Canopy fraction, layer, and whole canopy non-protein N as a percentage of total N of 5-wk limpograss regrowth in 1988.

Canopy component	Sampling Date: 28 July	17 Aug.	7 Sept.	28 Sept.	Mean
	g NPN kg^{-1} total N				
Fraction					
ULL	140	158	213	236	187a[+]
ULS	153	180	227	247	202a
LLL	82	180	238	252	182a
LLS	147	168	233	258	208a
Mean (15.0)[§]	133[¶]	181[¶]	227	248	(11.5)[‡]
Layer					
Upper	144	167	220	241	193x[#]
Lower	128	185	235	258	204x
Mean (17.8)[‡‡]	138[§§]	181[§§]	228	248	(5.8)[++]
Whole canopy					
(18.8)[¶¶]	138[##]	182	228	251	

[+] Fraction means over dates followed by the same letter are not different ($P \leq 0.05$).
[‡,§] Standard errors for fraction means over dates and date means over fractions, respectively.
[¶] Date mean over fractions differed from that on 7 September ($P \leq 0.05$).
[#] Layer means over dates did not differ ($P \geq 0.05$).
[++,‡‡] Standard errors for layer means over dates and date means over layers, respectively.
[§§] Date mean over layers differed from that on 7 September ($P \leq 0.05$).
[¶¶] Standard error for whole canopy date means.
[##] Mean differed from that on 7 September ($P \leq 0.05$).

Data for cell content true protein N expressed as a proportion of total N (g non-cell wall protein N kg^{-1} total N) showed no interaction between fraction and sampling date ($P = 0.313$, Table 5.9). Upper layer leaf, ULS, and LLL CCTPNTN did not differ but all tended to be greater than LLS (Table 5.10). Sampling date differences were detected for layer CCTPNTN such that it decreased over time. Upper layer CCTPNTN tended ($P = 0.074$) to be greater than that of LL. No sampling date effect was detected for whole canopy CCTPNTN, but whole canopy tended to decrease over time.

Discussion

Nitrogen distribution

Although overall CP concentration tended to be higher in 1988 than 1987 (Chapter IV), a similar distribution of N content was observed in both years. There was generally a uniform distribution of N content between the upper and lower halves of the sward canopy in the early part of the season, but for the latter part, UL N content was generally lower than LL. Results from Chapter IV suggest that the relatively high CP concentration of UL herbage was primarily responsible for UL CP (N) content whereas N content of the LL was attributable to high herbage mass.

Table 5.18. Canopy fraction, layer, and whole canopy call content (CC) true protein N as a percentage of total N of 5-wk limpograss regrowth in 1988.

Canopy component	Sampling Date: 28 July	17 Aug.	7 Sept.	28 Sept.	Mean	Contrast+: ULL	ULS
	(g CC true protein N kg^{-1} total N)						
Fraction							
ULL	214	226	175	170	196		
ULS	201	217	177	138	183		
LLL	200	227	222	179	207	NS	NS
LLS	176	152	115	120	141		*
Mean (11.1)§	198¶	206¶	172	152	(15.6)‡		
Layer							
Upper	210	222	176	159	192#		
Lower	186	171	140	136	158		
Mean (14.5)‡‡	188§§	186§§	158	148	(15.7)++		
Whole canopy	196	196	154	143	NS		

*,NS P ≤ 0.05 and P > 0.05, respectively.
+ Preplanned single df contrasts to test differences in fraction means over dates.
‡,§ Standard errors for fraction means over dates and date means over fractions, respectively.
¶ Date mean over fractions differed from that on 7 September (P ≤ 0.05).
# Layer means over dates did not differ (P ≥ 0.05).
++,‡‡ Standard errors for layer means over dates and date means over layers, respectively.
§§ Date mean over layers differed from that on 7 September (P ≤ 0.05).

In this study, seasonal variation in N content was more easily identified when the limpograss sward canopy was partitioned and analyzed by layer and by fraction rather than when analyzed on a whole canopy basis. Our data show that the distribution of N within a limpograss sward canopy is a function of both leaf and stem CP concentration and the relative proportions of leaf and stem material within different horizontal layers of the canopy.

Detergent fiber nitrogen concentration

Results indicate that there were plant part and layer differences in both N concentration of cell wall constituents and the proportion of total N associated with cell wall. The N concentration of leaf NDF was more than twice as great as for stem. Sanderson and Wedin (1989b) reported a similar difference between leaf and stem NDFN for timothy (Phleum pratense L.) and bromegrass. These authors (1989a) attributed decreases in NDFN and ADFN over time to increases in detergent fiber concentration. Our data suggest that the difference in NDFN and ADFN concentration between leaf and stem cannot be explained by the respective differences in NDF and ADF concentrations, alone. Differences in CP (total N) concentration between leaf and stem (Chapter IV) followed differences in NDFN and ADFN and they appeared to be related. When expressed as a percentage of total N, our results

indicate that limpograss cell wall N constituted 60 to 70% of the total N within leaf and stem fractions and that NDFNTN was generally higher in stem than leaf. Less than 16% of the total N in bromegrass has been shown to be associated with NDF (Sanderson and Wedin, 1989b), but no indication was given as to the relative contributions of leaf and stem to total herbage NDFNTN. Brown et al. (1988) reported that 58% of the total N in four Cynodon varieties was associated with NDF in whole plant samples. Between 27 and 31% of the total N in four temperate grasses has been shown to be associated with NDF (Abdalla et al., 1988b). Perennial ryegrass (Lolium perenne L.) cell wall has been reported to contain 10% of total N (Wilman et al., 1977). Thus, our data show that limpograss has a greater proportion of its N in the NDF fraction than previously reported for tropical grasses, and a much greater proportion than for temperate species. With respect to animal performance responses presented in Chapter III, there was no consistent relationship between seasonal variation in NDFNTN and seasonal changes in animal performance on LG pasture.

Acid detergent fiber N concentration for leaf and stem ranged from 2 to 4 g N kg^{-1} ADF and was similar to that reported by Sanderson and Wedin (1989b) for temperate grasses. Brown et al. (1988) reported that ADFN for four Cynodon varieties averaged from 10 to 20 g N kg^{-1} ADF and represented approximately 13% of total N. Eight-week

limpograss regrowth was reported to contain 1 g N kg^{-1} ADF on a total herbage basis (Brown, 1987). Our results also indicate that the relatively high proportion of stem N that was associated with ADF is more a function of low total N concentration rather than a high stem ADFN concentration. On a whole canopy basis, approximately 14% of total N was associated with ADF and is presumed to be indigestible (Van Soest, 1982). This suggests that in addition to the relatively low CP concentration that is often observed with limpograss, a substantial portion of the total CP is indigestible. This further diminishes the nutritive value of limpograss in terms of its ability to supply N to ruminant diets. As with NDFNTN, seasonal variation in ADFNTN on LG pasture showed little relationship to seasonal changes in animal performance that were presented in Chapter III.

Reports in the literature on the proportion of plant N that is associated with cell wall constituents have either been on a whole canopy basis or on a plant part basis. Our results indicate that there is non-uniform vertical distribution of cell wall-bound N. Upper layer NDFNTN and ADFNTN were 622 and 100 g kg^{-1}, while LL concentrations were 669 and 158, respectively. Differences in plant parts as well as relative proportion of plant parts within canopy layers appear to contribute to this non-uniform distribution. The ability to ascertain spatial variation in forage

nutritive value may be important when assessing the prehension of plant N by grazing animals.

Cell content nitrogen

Non-cell wall N in plant herbage is primarily comprised of cytoplasmic and chloroplastic protein and NPN components (Van Soest, 1982). Goering and Van Soest (1970) have suggested that extraction of NPN can be accomplished by refluxing the plant tissue in hot water, assuming that only NPN components are removed. We have attempted to improve on the accuracy of this estimate by quantifying true protein that was removed in the hot water filtrate during extraction and adjusting NPN estimates accordingly. Approximately 19% of the total N within each fraction was estimated to be in NPN form, suggesting that NPN content remained relatively constant regardless of CP concentration. Van Soest (1982) indicated that NPN as a percentage of total N in grasses was in the range of from 14 to 34%. Our results for 1 yr fall within this range. There is little reference to NPN in the literature, but our data suggest that NPN constitutes a significant portion of the total N in limpograss.

There are few reports on the proportion of true protein in the non-cell wall portion of forages. A major component of the soluble proteins in plant material is the fraction 1 leaf protein, ribulose-1,5-bisphosphate carboxylase. Brady

(1976) suggested that fraction 1 leaf protein can account for up to 50% of the total leaf protein in temperate species. Our results indicate that fraction 1 leaf protein in limpograss probably accounts for less than 20% of total leaf protein.

Summary and Conclusions

The objectives in this study were to characterize the form and distribution of N in a rotationally-grazed limpograss pasture. The N in limpograss pasture varies in its form and distribution and is dependant on plant part and the relative DM contribution of individual plant parts to the canopy. A greater proportion of total N is found in the stem fraction due to the greater contribution of stem than leaf to total herbage mass. This occurs despite N concentration in leaf being much higher than in stem. Because grazing animals tend to preferentially select leaf material, their ability to prehend CP on rotationally-grazed limpograss pasture may be more directly related to limpograss canopy structure than to whole canopy CP concentration.

Compared with temperate species that have less than 30% of total N in the cell wall fraction, 60 to 70% of limpograss N is associated with cell wall constituents. A significant amount of this N (> 20%) is bound in an indigestible form, particularly in the lower part of the canopy, suggesting that

whole canopy CP data for limpograss have limited value for assessing protein status of diets of grazing cattle.

We conclude that there is diversity in the forms of N and their distribution in a limpograss sward canopy and that seasonal variation in these attributes is observed. However, there appears to be little relationship between the seasonal variation in limpograss N fore and distribution with respect to seasonal changes in animal performance on limpograss pasture. Detailed assessment of tropical grass sward canopies may be necessary for a more useful description of forage N concentration and can provide more conclusive evidence of the relationship between pasture N status and animal performance under grazing.

CHAPTER VI
GENERAL DISCUSSION

The purpose of this section is to discuss some of the broader implications of this research in terms of both practical and research applications. The primary objective of these studies was to determine the role of protein accessibility (i.e., ease of prehension) and palatability in the summer slump phenomenon on 'Florsita' limpograss [Hemarthria altissima (Poir.) Stapf et C.E. Hubb.] pasture. One approach to determining if there is inadequate protein in the diet of grazing animals is to supplement with protein. Although a positive response to protein supplementation was observed on a seasonal basis, the corn-urea ration did not eliminate the slump in animal performance during the specific period of the season when lowest performance was observed with unsupplemented steers. Thus, the supplementation study suggests that inadequate dietary CP is not the only contributor to the summer slump condition, at least with Florelta limpograss under rotational-grazing management. Protein supplementation with corn-urea appears to be an effective alternative to growing a legume (Aeschynomene americana L.) in association with limpograss to improve seasonal production. One of the major advantages of supplementation over a grass-annual legume association is its

reliability and its independence from adverse environmental conditions that can impede the successful establishment of the legume component. Whether or not protein supplementation is economically sound in this situation requires further study. In addition, under these experimental conditions, great care was taken to ensure that each animal received the appropriate amount of supplement each day. It may prove to be difficult to regulate the administering of such small quantities of supplement in an actual livestock production system.

The results from characterizing the form and distribution of plant N indicate that inadequate amounts of available protein may have contributed to the observed slump in performance in each of 2 yr. This inadequacy of protein appears to be as much a function of the non-uniform distribution of N in the sward canopy, where a large portion of the total N is associated with the basal stem, as it is overall low CP concentration.

Perhaps the most significant findings in this research were the extent of non-uniform N distribution within the sward canopy and the relatively high proportion of limpograss N that is associated with cell wall constituents. When one considers the generally low CP concentration of limpograss along with the large proportion of the N that is either indigestible or associated with stem in the basal region of the canopy, the nutritive value of limpograss with respect to

CP appears to be quite marginal. This may also be true of other tropical grasses that have been shown to be relatively low in overall CP concentration, and warrants investigation.

From a research standpoint, our data suggest that there is much to be gained from a more descriptive assessment of pasture forage. Sward canopy structure has primarily been of interest to those investigating grazing behavior in the context of DM intake. Our data show that the ability of grazing animals to prehend specific plant nutrients (e.g., protein) may be more related to how nutrients are distributed throughout the sward canopy than to the overall concentration of a particular nutrient in the sward. Our results also illustrate the limitations of whole canopy data in assessing the nutritive value of forage grasses under grazing conditions.

The research presented here has provided the author with unique challenges as a forage agronomist and insight into the animal scientist's perspective. His greatest challenge has been the necessity of keeping the grazing ruminant at the focal point and as the common denominator throughout this research. The interface between plant and animal has been duly recognized and appreciated. It is this author's belief that the interface between the forage agronomist and animal scientist should be pursued with much enthusiasm.

LITERATURE CITED

Abdalla, M.D., D.G. Fox, and R.R. Seamsy. 1988a. Protein distribution in four cool-season grass variatias alone or in combination with trafoil. J. Anim. Sci. 66:2325-2329.

Abdalla, M.D., D.G. Fox, and R.R. Seamsy. 1988b. Variation in protain and fiber fractions in pasture during tha grazing saason. J. Anim. Sci. 66:2663-2667.

Adjei, M.B., P. Mislevy, K.H. Quesenberry, and W.R. Ocumpaugh. 1988. Grazing frsquancy affects on forags production, quality, parsistance and crown total non-structural carbohydrate reserves of limpograss. Proc. Soil Crop Sci. Soc. Florida. 47:233-236.

Akin, D.E., S.L. Palss, L.L. Rigsby, and M.R. Snook. 1987. Temparature affects on leaf anatomy, phenolic acids, and tissue digestibility in tall fascue. Agron. J. 79:271-275.

Allden, W.G., and I.A. McD. Whittaker. 1970. The datarminants of harbags intaks by grazing sheep: Tha interrelationships of factors influencing harbags intska snd svsilability. Aust. J. Agric. Res. 21:755-766.

Arnold, G.W. 1960. Salactive grazing by sheep of two forags spacias at diffarent stagas of growth. Aust. J. Agric. Res. 11:1026-1033.

Barth, R.M., J.R. McLaran, H.A. Fribourg, and L.A. Carvar. 1982. Crude protain contant of forags consumad by staars grazing nitrogan-fertilized bermudagrass and orchardgrass-ladino clovsr pastures. J. Anim. Sci. 55.1008-1014.

Barthram, G.T., and S.A. Grant. 1984. Defoliation of ryegrass-dominatad swards by sheep. Grass Forage Sci. 39:211-219.

Batss, D.R., G.A. Morantes, and J.E. Moore. 1988. Nitrogan utilization of lambs fed limpograss supplemantad with molassas-urea or laguma protain supplements. Nutr. Rep. Int. 38.487-499.

Baever, D.E., and D.J. Thompson. 1981. The effect of drying and processing red clover on the digestion of the energy and nitrogen moieties in the alimentary tract of sheep. Grass Forage Sci. 36.211-219.

Blaser, R.E. 1964. Symposium on forage utilization: Effects of fertility levels and stage of maturity on forage nutritive value. J. Anim. Sci. 23:246-253.

Blaxter, K.L., F.W. Wainman, and R.S. Wilson. 1961. The regulation of food intake by sheep. Anim. Prod. 3:51.

Bornemen, W.S., D.E. Akin, and W.P. Van Eseltine. 1996. Effect of phenolic monomers on ruminal bacteria. Appl. Env. Microbiol. 52:1331-1339.

Bradford, M.M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Anal. Biochem. 72:248-254.

Brady, C.J. 1976. Plant proteins, their occurrence, quality and distribution. In T.M. Sutherland, J.R. McWilliam, and R.A. Leng (eds.) From Plant to Animal Protein. Univ. of New England Publ. Unit, Armidale.

Brown, W.F., J.D. Phillips, and D.B. Jones. 1997. Ammoniation or cane molasses supplementation of low quality forages. J. Anim. Sci. 64:1205-1214.

Brown, W.F., W.D. Pitman, and P. Wislavy. 1998. Intake and digestibility of, and performance by cattle grazing Cynodon varieties. Nur. Rep. Int. 39:1201-1209.

Bruckental, I., H. Tegeri, S. Amir, H. Kennit, and S. Zamwell. 1996. The effect on the performance of dairy cattle of plant protein concentrates and of urea or urea-phosphate supplementation in the diet. Anim. Prod. 43:73-92.

Buttery, P.J., and D. Lewis. 1992. Nitrogen metabolism in the rumen. In D.J. Thompson, D.E. Baever, and K.G. Gunn (eds.) Forage Protein in Ruminant Animal Production. Occasional Publ. No. 6, Br. Soc. Anim. Prod.

Campling, R.C., M. Freer, and C.C. Balch. 1962. Factors affecting the voluntary intake of food by cows. 3. The effect of urea on the voluntary intake of oat straw. Br. J. Nutr. 16:115-124.

Chacon, E., and T.H. Stobbs. 1976. Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. Aust. J. Agric. Res. 27:709-727.

Cherry, John P. 1981. Protein functionality in foods. ACS Symp. series 147. Amer. Chem. Soc., Washington, D.C.

Christiansen, S., O.C. Ruelke, W.R. Ocumpaugh, R.R. Quesenberry, and J.E. Moore. 1988. Seasonal yield and quality of 'Bigalta', 'Redalta', and 'Floralta' limpograss. Trop. Agric. 65:49-55.

Clanton, D.C. 1978. Non-protein nitrogen in range supplements. J. Anim. Sci. 47:765-779.

Cocimano, M.R., and R.A. Leng. 1967. Metabolism of urea in sheep. Br. J. Nutr. 21:553-563.

Cohen, R.D.H., and A.O. O'Brien. 1974. Beef production from three pastures at Grafton N.S.W. Trop. Grassld. 8:71-79.

Colburn, R.W., and J.L. Evans. 1967. Chemical composition of the cell-wall constituent and acid detergent fiber fractions of forages. J. Dairy. Sci. 50:1130-1135.

Conrad, H.R. 1966. Symposium on factors influencing the voluntary intake of herbage by ruminants: Physiological and physical factors limiting feed intake. J. Anim. Sci. 25:227-235.

Coombe, J.E., and D.E. Tribe. 1963. The effects of urea supplements on the utilization of straw plus molasses diets by sheep. Aust. J. Agric. Res. 14:70-92.

Crooker, B.A., C.J. Sniffen, W.H. Hoover, and L.L. Johnson. 1978. Solvents for soluble nitrogen measurements in feedstuffs. J. Dairy Sci. 61:437-447.

Oelnum, B., and J.G.P. Dirven. 1972. Climate, nitrogen and grass. 5. Influence of age, light intensity and temperature on the production and chemical composition of Congo grass (Brachiaria ruziziensis Germain et Everard). Neth. J. Agric. Sci. 20.125-132.

Dixon, R.M., and J.V. Nolan. 1983. Studies of the large intestine of sheep. 3. Nitrogen kinetics in sheep given chopped lucerne (Medicago sativa). Br. J. Nutr. 50.757-76a.

Dixon, R.M., and J.V. Nolan. 1986. Nitrogen and carbon flows between caecum, blood and rumen in sheep given chopped lucerne (Medicago sativa). Br. J. Nutr. 55:313-332.

Driedger, A., and E.E Hstfield. 1972. Influence of tsnnins on the nutritive velus of soybean meal for rumlsnts. J Anim. Sci. 34:465-468.

Egsn, A.R. 1965. Nutritional ststus snd intake rsgulstion in shssp III. The relstlonshlp betwsen improvement of nitrogen ststus snd incrssse in voluntsry intske of low-protsin roughsgss by shesp. Aust. J. Agr. Res. 16:463-472.

Egsn, J.K., snd P.T. Doyls. 1985. Effect of intrsruminal infusion of urss on the response in voluntary food intske by shssp. Aumt. J. Agric. Res. 36:483-495.

El-Shszly, K., B.A. Dehority, snd R.R. Johnson. 1961. Effect of stsrch on the dlgestion of cellulose in vitro snd in vivo by rumen microorgsnisms. J. Anim. Sci. 20:268-273.

Elllot, R., snd D.G. Armstrong. 1982. The effsct of urss snd urss plus sodium sulphate on microbisl protsin productlon in ths rumsn of sheep given diets hlgh in slksll-trssted bsrley strsw. J. Agr. Scl. (Csmb.) 99.51-59.

Ellis, J.L., R.E. Morrow, G.E Gsrner, J.A. Strickxr, snd M.R. Ellersleck. 1983. Supplemental feedlng of spring-calvlng cows on tall fescus or tall fescue-red clover pssturss. J. Anim. Sci. 57:535-541.

Erssmus, L.J., J. Prinsloo, snd H.H. Msissner. 1988. The establishment of s protein degrsdability dsta bass for dsiry cattle ueing the nylon bag technique. I. Protein esurces. S. Afr. J. Anim. Sci. 18:23-29.

Ernst, A.J., J.F. Llmpus, snd P.K. O'Rourke. 1975. Effscts of supplements of molssses snd ures on lntake snd digestlblllty of natlvs pssture hay by steers. Aust. J. Exp. Agric. Anim. Husb. 15:451-455.

Evers, G.W. 1985. Forsge snd nitrogen contributions of srrowlesf snd subterransan clovers overseeded on bersudsgrsss snd bshlsgrsss. Agron. J. 77:960-963.

Ferguson, K.A., J.A. Hemsley, snd P.J. Rsls. 1967. Nutritlon snd wool growth. ths effect of protactlng distary protsln from mlcroblsl degradation in ths rumsn. Aust. J. Agric. Scl. 30:215.

Gsllsher, R.N., C.O. Weldon, and J.G. Futrsl. 1975. An aluminum block dlgester for plsnt snd soil snslysls. Soil Scl. Soc. Amsr. Proc. 39:803-806

Goering, H.K., C.H. Gordon, R.W. Hemken, D.R. Waldo, P.J. Van Soest, and L.W. Smith. 1972. Analytical estimates of nitrogen digestibility in heat damaged forages. J. Dairy Sci. 55:1275-1280.

Goering, H.K., and P.J. Van Soest. 1970. Forage fiber analyses (apparatus, reagents, procedures and some applications). USDA-ARS Agr. Handbook No. 379.

Golding, E.J., J.E. Moore, D.E. Franks, and O.C. Ruelke. 1976. Formulation of hay-grain diets for ruminants. II. Depression in voluntary intake of different quality forages by limited grain in sheep. J. Anim. Sci. 42:717-723.

Hamblaton, L.C. 1977. Semiautomated method for simultaneous determination of phosphorous, calcium and crude protein in animal feeds. J.A.O.A.C. 60:845-852.

Hammond, A.C. 1987. Chemical, anatomical and other antiquality factors limiting forage utilization. pp. 59-65. In J.E. Moore, K.H. Quesenberry, and M.W. Micheud (eds.) Forage-Livestock Research Needs in the Caribbean Basin. Caribbean Basin Advisory Group, Univ. of Florida, Gainesville. Lib. Cong. no. 87-70440.

Hargreaves, A., J.T. Huber, J. Arroyoluna, and L. Kung, Jr. 1984. Influence of adding ammonia to corn stalklage on feeding value for dairy cows and on fermentation changes. J. Anim. Sci. 59:567-575.

Harrison, D.G., D.E. Beever, D.J. Thompson, and D.F. Osbourn. 1973. The influence of diet upon the quantity and types of amino acids entering and leaving the small intestine of sheep. J. Agric. Sci. (Camb.) 81:391-401.

Harrison, D.G., D.E. Beever, D.J. Thompson, and D.F. Osbourn. 1975. Manipulation of rumen fermentation in sheep by increasing the rate of flow of water from the rumen. J. Agric. Sci. (Camb.) 85:93-101.

Hemsley, J.A., and H.J. Moir. 1963. The influence of higher volatile fatty acids on the intake of urea-supplemented low quality cereal hay by sheep. Aust. J. Agric. Res. 14:509-517.

Heepell, H.B., and M.P. Bryant 1979. Efficiency of rumen microbial growth: influence of some theoretical and experimental factors on Y_{ATP}. J. Anim. Sci. 49:1640-1659.

Hewitt, E.J., D.P. Nuckissby, A.F. Mann, B.A. Notton, and G.J. Rucklidge. 1979. Regulation of nitrate assimilation in plants. pp. 255-287. In E.J. Hewitt and C.V. Cutting (eds.) Nitrogen Assimilation of Plants. Proc. Sixth Long Ashton Symp., Univ. of Bristol. Academic Press, London, England.

Hodgson, J. 1985. The control of herbage intake in the grazing ruminant. Proc. Nutr. Soc. 44:339-346.

Hogan, J.P., and R.H. Weston. 1981. Laboratory methods for protein evaluation. pp. 75-87. In J.L. Wheeler and R.D. Mochrie (eds.) Forage Evaluation: Concepts and Techniques. CSIRO.

Horn, G.W., and F.T. McCollum. 1987. Energy supplementation of grazing ruminants. pp. 125-136. In Proc. Grazing Livestock Nutrition Conf. Jackson, WY.

Hume, I.D., R.J. Moir, and M. Somers. 1970. Synthesis of microbial protein in the rumen. I. Influence of the level of nitrogen intake. Aust. J. Agric. Res. 21:283-296.

Hunter, R.A., and R.D. Siebert. 1980. The utilization of spear grass (Heteropogon contortus). IV. The nature and flow of digesta in cattle fed on spear grass alone and with protein or nitrogen or sulfur. Aust. J. Agric. Res. 31:1037-1047.

Johnson, R.R. 1976. Influence of carbohydrate solubility on non-protein nitrogen utilization in the ruminant. J. Anim. Sci. 43:184-191.

Kempton, T.J., and R.A. Leng. 1979. Protein nutrition of grazing lambs. I. Responses in growth and rumen function to supplementation of a low-protein-cellulosic diet with either urea, casein or formaldehyde-treated casein. Br. J. Nutr. 42:289-302.

Kennedy, P.M., and L.P. Milligan. 1980. The degradation and utilization of endogenous urea in the gastro-intestinal tract of ruminants. A review. Can. J. Anim. Sci. 60:205.

Krishnamoorthy, U., C.J. Sniffen, M.D. Stern, and P.J. Van Soest. 1983. Evaluation of a mathematical model of rumen digestion and an in vitro simulation of rumen proteolysis to estimate the rumen undegraded nitrogen content of feedstuffs. Br. J. Nutr. 50:555-568.

Kwan, K., C.E. Coppock, G.B. Lake, M.J. Feltman, L.E. Chase, and R.E. McDowell. 1977. Use of urea by early post-partum Holstein cows. J. Dairy Sci. 60:1706-1724.

Lee, G.J., D.W. Bennaway, J.V. Nolan, and R.A. Leng. 1987. Responses to nitrogen and maize supplements by young cattle offered a low-quality pasture hay. Aust. J. Agric. Res. 38:195-207.

Leng, R.A., and J.V. Nolan. 1984. Nitrogen metabolism in the rumen. J. Dairy Sci. 67:1072-1089.

Lowry, J.B., and E.A. Sumpter. 1987. Effect of free phenolic acids on rumen function in sheep. pp. 51-52 In Mary Rose (ed.) Herbivore Nutrition Research, Second Int. Symp. on the Nutrition of Herbivores. Univ. of Queensland, Brisbane, Australia.

Madsen, J., and T. Hvelplund. 1985. Protein degradation in the rumen. A comparison between in vivo nylon bag, in vitro and buffer measurements. Acta Agric. Scand. 25:103.

Mae, T., and K. Ohira. 1982. Relation between leaf age and nitrogen incorporation in the leaf of the rice plant (Oryza sativa L.). Plant Cell Physiol. 23:1019-1024.

Mahadevan, S., J.D. Erfle, and F.D. Sauer. 1980. Degradation of soluble and insoluble protein by Bacteroides amylophilus protease and by rumen microorganisms. J. Anim. Sci. 50:723-728.

Mangan, J.L., R.L. Vetter, D.J. Jordan, and P.C. Wright. 1976. The effect of condensed tannins of sainfoin (Onobrychis viciaefolia) on the release of soluble leaf protein into the food bolus of cattle. Proc. Nutr. Soc. 35:95A-97A.

Mangan, J.L., and J. West. 1977. Ruminal digestion of chloroplasts and the protection of protein by glutaraldehyde treatment. J. Agric. Sci. Camb. 89:13-15.

Mannetje, L., 't, and J.F. Ebersohn. 1980. Relations between sward characteristics and animal production. Trop. Grassld. 14:273-279.

Marsh, W.H., B. Fingerhut, and H. Miller. 1965. Automated and manual direct methods for the determination of blood urea. Clin. Chem. 11:624-627.

Marten, G.C. 1969. Measurement and significance of forage palatability. Proc. National Conf. Forage Quality Eval. and Util., Nebraska Center Cont. Educ., Lincoln, NE.

Marten, G.C. 1978. The animal-plant complex in forage palatability phenomena. J. Anim. Sci. 46:1470-1477.

Matches, A.G. 1970. Pasture research methods. pp. 151-182. In R. F Barnes, D.C. Clanton, C.H. Gordon, T.J. Klopfenstein, and D R. Waldo (eds.) Proc. Nat. Conf. Forage Quality Eval. and Util., Nebraska Center for Continuing Educ , Lincoln, NE.

Mayland, H.F., T.R. Kreasr, and W T. Johnson. 1987. Trace elesents in the nutrition and immunoiogical response of grazing iivestock. Proc. Grazing Livestock Nutr. Conf., Jackson, WY.

McAllen, A.B., and E.P. Griffith. 1987. The effects of different sources of nitrogen supplementation on the digestion of fiber components in the rumen of steers. Ani. Feed Sci. Tech. 17:65-73.

Miiford, R. 1960 Criteria for expressing nutritional values of subtropicai grasses. Aust. J. Agric. Res. 11:121-137.

Miiford, R., and K.P. Heydock. 1965. The nutritive value of protein in subtropical pasture species grown in southeast Queensiand. Aust. J. Exp. Agr. Anim. Husb. 5:13-17.

Milford, R., and D.J. Minson. 1966a. Intake of tropical pasture species. p. 815-822. Proc. IX Int. Grassi. Cong. Sao Pauio, Brazil

Milford, R., and D.J. Minson. 1966b. Determinants of feeding vaiue of pasture and supplementai feed. Proc. Aust. Soc. Anim. Prod. 6:319-329.

Minson, D.J. 1971. The nutritive vaiue of tropicai pastures. J. Aust. Inst. Agr. Sci. 37:255-263.

Minson, D.J. 1980. Nutritional differences between tropicai and temperate pastures. p. 143-157. In. F.H.W. Morley (ed.) Grazing Animals. Elsevier Scientific Publishing Co., Amsterdam.

Minson, D.J. 1983. Forage quaiity: Assessing the plant-animai complex. pp. 23-27. Proc. XIV Int. Grassiand Cong., Lexington, KY. 15 June - 24 June 1981. Westview Press, Boulder, CO.

Minson, D.J., and R. Miiford. 1967. The voiuntary intake and digestibiiity of diets containing different proportions of legume and mature Pangoie grass (Digitaria decumbens). Aust. J. Exp. Agr. Anim. Husb. 7:546-551.

Moore, J.E. 1983. Remarks of discussion leader, J.E. Moore. pp. 27-28. Proc. XIV Int. Grassland Cong., Lexington, KY. 15 June - 24 June 1981 Westview Press, Boulder, CO.

Moore, J.E., and G.O. Mott. 1973. Structural inhibitors of quality in tropical grasses. pp. 53-98. In A.G. Matches (ed.) Anti-quality Components of Forages. CSSA Special Publ. 4, Crop Sci. Soc. Am., Madison, WI.

Moore, J.E., and G.O. Mott. 1974. Recovery of residual organic matter from in vitro digestion of forages. J. Dairy Sci. 57:1258-1259.

Moore, J.E., L.E. Sollenberger, G.A. Morantes, and P.T. Beede. 1987. Canopy structure of Aeschynomene americana-Hemarthria altissima pastures and ingestive behavior of cattle. pp. 93-114. In F.P. Horn, J. Hodgson, J.J. Mott, and R.W. Brougham (eds.) Grazing-lands Research at the Plant-animal Interface. Proceedings of a special session, Winrock International, Morrilton, AR.

National Research Council. 1985. Ruminant Nitrogen Usage. National Academy Press, Washington, D.C.

Nolan, J.V., and J.C. Macrae. 1976. Absorption and recycling of nitrogenous compounds in the digestive tract of sheep. Proc. Nutr. Soc. 35:110A.

Nugent J.R.A., and J.L. Mangan. 1981. Characteristics of the rumen proteolysis of fraction I (18S) leaf protein from lucerne (Medicago sativa L.). Br. J. Nutr. 46:39-58.

Nugent, J.R.A., W.T. Jones, D.J. Jordan, and J.L. Mangan. 1983. Rates of proteolysis in the rumen of the soluble proteins casein, fraction I (18S) leaf protein, bovine serum albumin and bovine submaxillary mucoprotein. Br. J. Nutr. 50:357-368.

Oldham, J.D., and T. Smith, 1982. Protein-energy interrelationships for growing and for lactating cattle. In E.L. Miller and I.H. Pike (eds.) Protein Contributions of Feedstuffs for Ruminants: Applications to Feed Formulation. Butterworth Scientific, Boston.

Orskov, E.R. 1982. Protein nutrition in ruminants. Academic Press, New York.

Paterson, R.K. 1987. Nitrogen supplementation of grazing livestock. Proc. Grazing Livestock Nutrition Conf. Jackson, WY.

Peterson, M.K., D.C. Clanton, and R. Britton. 1985. Influence of protein degradability in range supplements on abomasal nitrogen flow, nitrogen balance and nutrient digestibility. J. Anim. Sci. 60:1324-1329.

Pichard, G., and P.J. Van Soest. 1977. Protein solubility of ruminant feeds. pp. 91-98. Proc. Cornell Nutr. Conf.

Poppi, D.P., D.J. Minson, and J.H. Ternouth. 1980. Studies of cattle and sheep eating leaf and stem fractions of grasses. I. The voluntary intake, digestibility and retention time in the reticulo-rumen. Aust. J. Agric. Res. 32:99-108.

Power, J.F. 1986. Nitrogen cycling in seven cool-season perennial grass species. Agron. J. 78:681-687.

Quesenberry, M.H., W.R. Ocumpaugh, O.C. Ruelke, L.S. Dunavin, and P. Mislevy. 1984. Florsite: A limpograss selected for yield and persistence in pastures. Fla. Agric. Exp. Stn. Circ. S-312. University of Florida, Gainesville.

Raymond, W.F. 1968. Components in the nutritive value of forages. pp. 47-62. ASA Special Publ. No. 13. Madison, WI.

Raymond, W.F. 1969. The nutritive value of forage crops. Adv. Agron. 21:1-108.

Redman, R.G., H.C. Kellaway, and J. Leibholz. 1980. Utilization of low quality roughages: effects of urea and protein supplements of differing solubility on digesta flows, intake and growth rate of cattle eating oaten chaff. Br. J. Nutr. 44:343-354.

Rees, M.C., D.J. Minson, and P.W. Smith. 1974. The effect of supplementary and fertilizer sulphur on voluntary intake, digestibility, retention time in the rumen, and site of digestion of pangola grass in sheep. J. Agric. Sci. Camb. 82:419-422.

Robbins, C.T., T.A. Hanley, A.E. Hagerman, O. Hjeljord, D.L. Baker, C.C. Schwartz, and W.W. Mautz. 1987. Role of tannins in defending plants against ruminants: Reduction in protein availability. Ecology. 68(1):98-107.

Ruelke, O.C., and M.H. Quesenberry. 1983. Effects of fertilization timing on the yields, seasonal distribution and quality of limpograss forage. Soil Crop Sci. Soc. Florida. 42:1321.

Rush, I.G., and R. Totusek. 1976. Supplemental value of feedgrade blurst and urea-molasses for cows on dry winter grass. J. Anim. Sci. 42:497-505.

Rusland, G.A., L.E. Sollenberger, R.A. Albrecht, C.S. Jones, Jr., and L.V. Crowder. 1988. Animal performance on limpograss-aeschynomene and nitrogen fertilized limpograss pastures. Agron J. 80:957-962.

Russell, J.B., and B.B. Hespell. 1981. Microbial rumen fermentation. J. Dairy Sci. 64:1153-1169.

Russell, R.E., C.J. Sniffen, and P.J. Van Soest. 1983. Effects of carbohydrate limitation on degradation and utilization of casein by mixed rumen bacteria. J. Dairy Sci. 66:763-775.

Sanderson, M.A., and W.F. Wedin. 1989a. Nitrogen concentrations in the cell wall and ligno-cellulose of smooth bromegrass herbage. Grass Forage Sci. 44:151-158.

Sanderson, M.A., and W.F. Wedin. 1989b. Nitrogen in the detergent fibre fractions of temperate legumes and grasses. Grass Forage Sci. 44:159-168.

Satter, L.D., and L.L. Slyter. 1974. Effect of ammonia concentration on rumen microbial protein production in vivo. Br. J. Nutr. 32:199-208.

Schank, S.C., M.A. Klock, and J.E. Moore. 1973. Laboratory evaluation of quality in subtropical grasses. II. Genetic variation among Hemarthria in in vitro digestion and stem morphology. Agron. J. 65:256-258.

Schneichel, M., C. Lascano, and J.H. Wenliger. 1988a. Qualitative and quantitative intake of steers grazing native grasslands supplemented with a legume pasture in the eastern plains of Columbia. I. Plant part composition and crude protein content of forage on offer and selected by esophageal fistulated steers. J. Anim. Breed. Genet. 105:61-69.

Schneichel, M., C. Lascano, and J.H. Wenliger. 1988b. Qualitative and quantitative intake of steers grazing native grasslands supplemented with a legume pasture in the eastern plains of Columbia. II. Legume selection, nutrient intake and grazing behaviour. J. Anim. Breed. Genet. 105:154-159.

Simpson, Richard J. 1986. Translocation and metabolism of nitrogen: whole plant aspects. pp. 71-96. In H. Lambers, J.J. Neeteson, and I. Stulen (Eds.) Fundamental, Ecological and Agricultural Aspects of Nitrogen Metabolism in Higher Plants. Martinus Nijhoff Publ., Dordrecht, Netherlands.

Smith, G.H. 1984. Conditions determining the need for supplemental nitrogen by cattle grazing dry forage in temperate areas. Proc. Austr. Soc. Anim. Prod. 15:111-117.

Smith, R.H. 1979. Synthesis of microbial nitrogenous compounds in the rumen and their subsequent digestion. J. Anim. Sci. 49:1604-1614.

Sollenberger, L.E., W.R. Ocumpaugh, V.P.H. Euclides, J.E. Moore, K.H. Quesenberry, and C.S. Jones, Jr. 1988a. Animal performance on continuously stocked Pensacola' bahiagrass and Floralta' limpograss pastures. J. Prod. Agric. 1:216-220.

Sollenberger, L.E., G.H. Prine, W.R. Ocumpaugh, W.W. Hanna, C.S. Jones, Jr., S.C. Schank, and R.S. Kalmbacher. 1988b. 'Mott' Dwarf Elephantgrass: A high quality forage for the subtropics and tropics. Florida Agric. Exp. Stn. Circ. S-356.

Sollenberger, L.E., K.H. Quesenberry, and J.E. Moore. 1987a. Effects of grazing management on establishment and productivity of aeschynomene overseeded in limpograss pastures. Agron. J. 79:78-82.

Sollenberger, L.E., K.H. Quesenberry, and J.E. Moore. 1987b. Forage quality responses of an aeschynomene-limpograss association to grazing management. Agron. J. 79:81-89.

Sollenberger, L.E., G.A. Rualand, C.S. Jones, Jr., K.A. Albrecht, and K.L. Geiger. 1989. Animal and forage responses on rotationally grazed Floralta' limpograss and Pensacola' bahiagrass pasture. Agron. J. 81: (in press)

Stephanson, R.G.A., M.H. Weston, D.E. Margan, and J.P. Hogan. 1983. Intake and digestion of mature flinders grass (Iseilema spp.) by sheep and their response to the addition of urea and minerals. Aust. J. Agr. Res. 34:549-556.

Stern, M.D., and L.D. Satter. 1984. Evaluation of nitrogen solubility and the dacron bag technique as methods for estimating protein degradation in the rumen. J. Anim. Sci. 58:714-724.

Stobbs, T.H. 1973a. The effect of plant structure on the intake of tropical pastures. I. Variation in the bite size of grazing cattle. Aust. J. Agric. Res. 24:809-819.

Stobbs, T.H. 1973b. The effect of plant structure on the intake of tropical pastures. II. Differences in sward structure, nutritive value, and bite size of animals grazing Setaria anceps and Chloris gayana at various stages of growth. Aust. J. Agric. Res. 24:821-829.

Tamminga, S. 1979. Protein degradation in the forestomachs of ruminants. J. Anim. Sci. 49:1615-1630.

Taylor, J.C., and J.E. Rudman. 1966. The distribution of herbage at different heights in 'grazed' and 'dung patch' areas of a sward under two methods of grazing management. J. Agric. Sci. Camb. 66:29-39.

Van Der Aar, P.J., L.L. Berger, and G.C. Fahey. 1982. The effect of alcohol treatments on solubility and in vitro and in situ digestibilities of soymeal bean protein. J. Anim. Sci. 55:1175-1189.

Van der Walt, J.G., and J.H.F. Meyer. 1988. Protein digestion in ruminants. S. Afr. Tydskr. Vaek. 18:30-41.

Van Niekirk, B.D.H., and G.A. Jacobs. 1985. Protein, energy and phosphorous supplementation of cattle fed low-quality forage. S. Afr. Tydskr. Vaek. 15:133-136.

Van Soest, P.J. 1962. Estimation of forage protein digestibility and determination of the effects of heat-drying upon forages by means of the nitrogen content of acid-detergent fiber. J. Dairy Sci. 45:664 (abstract).

Van Soest, P.J. 1982. Nutritional ecology of the ruminant. O and B Books, Corvallis, OR.

Van Soest, P.J., C.J. Sniffen, D.R. Mertens, D.G. Fox, P.H. Robinson, and U. Krishnamoorthy. 1982. A net protein system for cattle: The rumen submodel for nitrogen. p. 265 In F.N. Owens (ed.) Protein Requirements for Cattle: Proceedings of an International Symposium, MP-109. Stillwater, OK. Division of Agriculture, Oklahoma State University.

Van't Klooster, A.T., and H.A. Boekhoit. 1972. Protein digestion in the stomachs and intestines of the cow. Neth. J. Agric. Sci. 20:272.

Ventura, M., J.E. Moore, O.C. Ruelke, and D.E. Franke. 1975. Effect of maturity and protein supplementation on voluntary intake and nutrient digestibility of Pangola digitgrass hays. J. Anim. Sci. 40:768-774.

Waldo, D.R., and H.K. Goering. 1976. Insolubility of proteins in ruminant feeds by four methods. J. Anim. Sci. 45:1580-1588.

Waldo, D.R., and N.A. Jorgensen. 1981. Forages for high animal production: Nutritional factors and effects of conservation. J. Dairy Sci. 64:1207-1228.

Wallace, R.J. 1983. Hydrolysis of ^{14}C-labelled proteins by rumen micro-organisms and by proteolytic enzymes prepared from rumen bacteria. Br. J. Nutr. 50:345-355.

Wallace, R.J., and J. Kopecny. 1983. Breakdown of diazotized proteins and synthetic substrates by rumen bacteria. Appl. Environ. Microbiol. 45:212-217.

Weston, R.H. 1971. Factors limiting the intake of feed by sheep. V. Feed intake and the productive performance of the ruminant iamb in relation to the quantity of crude protein digested in the intestines. Aust. J. Agr. Res. 22:307-320.

Williams, D.L., J.V. Whiteman, and A.D. Tillman. 1967. Urea utilization in protein supplements for cattle consuming poor quality roughages on the range. J. Anim. Sci. 26:807-815.

Wilman, D., M. Daly, A. Koocheki, and A.B. Lwoga. 1977. The effect of interval between harvests and nitrogen application on the proportion and digestibility of cell wall, cellulose, hemicellulose and lignin and on the proportion of lignified tissue in leaf cross-section in two perennial ryegrass varieties. J. Agric. Sci. (Camb.) 88:53-58.

Wilman, D., and P.T. Wright. 1978. The proportions of cell content, nitrogen, nitrate-nitrogen and water-soluble carbohydrate in three grasses in the early stages of regrowth after defoliation with and without applied nitrogen. J. Agric. Sci. (Camb.) 91:381-384.

Wilson, J.R., and D.J. Minson. 1980. Prospects for improving the digestibility and intake of tropical grasses. Trop. Grassld. 14:253-259.

Wohlt, J.E., and J.H. Clark. 1978. Nutritional value of urea versus preformed protein for ruminants. I. Lactation of dairy cows fed corn based diets containing supplemental nitrogen from urea and/or soybean meal. J. Dairy Sci. 61:902-915.

Wohlt, J.E., C.J. Sniffen, L.L. Johnson, and C.K. Walker. 1976. Nitrogen metabolism in wethers as affected by dietary protein solubility and amino acid profile. J. Anim. Sci. 42:1280-1289.

BIOGRAPHICAL SKETCH

James F. Holderbaum was born on 29 March 1960, in Linden, New Jersey. He is one of five sons of Paul and Janet Holderbaum and was raised in Linden until graduating from Linden High School in 1978. He received a B.S. degree in agricultural sciences from Cook College, Rutgers University in 1982 and was president of his graduating class.

Upon graduation, Jim worked for a dairy equipment sales and service center in southern New Jersey until enrolling at the University of Maryland in 1983. From 1983 to 1986, he worked as a research assistant under the direction of Dr. A. M. Decker at the University of Maryland and received his M.S. degree in Agronomy in 1986.

Jim enrolled at the University of Florida in the fall of 1986 and has served as a teaching assistant until 1989. He is currently a candidate for the Doctor of Philosophy degree and is a member of the American Society of Agronomy, the American Forage and Grassland Council, the Crop Science Society of America, and Gamma Sigma Delta, the Honor Society of Agriculture.

Jim is married to Sandra (Pilkerton) Holderbaum, and they have three children, James Brandon, Callen David, and Grace Ann.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy

Kenneth H. Quesenberry
Kenneth H. Quesenberry, Chairman
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Lynn E. Sollenberger
Lynn E. Sollenberger, Cochairman
Assistant Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Douglas B. Bates
Douglas B. Bates
Associate Professor of Animal Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

William E. Kunkle
Associate Professor of Animal Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John E. Moore
Professor of Animal Science

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December 1989

Jack L. Fry
Dean, College of Agriculture

Dean, Graduate School